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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years

G.A. Rose

Abstract: To examine overfishing and climate effects on depleted cod (*Gadus morhua*) stocks, a surplus production model based on reconstructions of cod catch in Newfoundland was used to describe biomass dynamics from 1505 to 2004. Productivity parameters r (population growth rate) and K (carrying capacity) were assigned by fitting model to survey biomass. Assumptions of fishery-only influences inferring constant, random, or depensatory parameters fared poorly (did not mimic history), as did climate influences indexed by tree ring growth. However, a model using both climate and depensation fared well, mimicking much documented history of Newfoundland cod, including declines during the Little Ice Age (mid- to late 19th century) and the stock collapses of the late 20th century, with a good fit to recent scientific surveys ($r^2 = 0.80$). This model suggests temporal differentiation between fishing and climate effects, including (*i*) declines during the Little Ice Age (1800–1880) caused by lower productivity, (*ii*) collapses in the 1960s caused by overfishing, (*iii*) collapses in the late 1980s caused by both, and (*iv*) rebuilding now hindered by depensatory effects of low numbers.

Résumé : Un modèle de production excédentaire basé sur des reconstitutions des prises de morues franches (*Gadus morhua*) à Terre-Neuve qui décrit la dynamique de la biomasse de 1505 à 2004 a servi à examiner les effets de la surpêche et du climat sur l'épuisement des stocks. L'ajustement du modèle à l'inventaire de la biomasse a permis d'évaluer les paramètres de productivité r (taux de croissance de la population) et K (stock limite). Les présuppositions basées sur les seuls effets de la pêche qui présument de l'existence de paramètres constants, aléatoires ou affectés par l'effet d'Allee (effet de groupe) ne donnent pas de bons résultats (elles ne reconstituent pas le déroulement historique de la situation); celles basées sur les seules influences climatiques déterminées par la croissance des anneaux des arbres ne fonctionnent pas non plus. Cependant, un modèle fondé conjointement sur le climat et l'effet d'Allee fonctionne bien et permet de reconstituer en grande partie l'histoire connue de la morue à Terre-Neuve, y compris les déclins durant la petite période glaciaire (du milieu à la fin du 19e siècle) et les effondrements de stocks de la fin du 20e siècle, et il s'ajuste bien aux inventaires scientifiques récents ($r^2 = 0,80$). Le modèle indique l'existence d'une différentiation dans le temps entre les effets de la pêche et du climat, en particulier, (*i*) des déclins durant la petite période glaciaire (1800–1880) dus à une productivité réduite, (*ii*) des effondrements de stocks dans les années 1960 à cause de la surpêche, (*iii*) des effondrements à la fin des années 1980 reliés aux deux facteurs et (*iv*) une récupération actuelle des stocks entravée par les faibles densités qui génèrent un effet d'Allee.

[Traduit par la Rédaction]

Introduction

Atlantic cod (*Gadus morhua*) stocks off Newfoundland were decimated from 1950 to 1990 by recruitment overfishing (for review, see Sinclair and Murawski 1997). However, climatic factors may have amplified declines through negative productivity change (Rice 2002) and may be impeding recovery. Productivity changes through reduced recruitment and growth (Drinkwater 2002) and sustained predation by harp seals (*Phoca groelandica*) have been implicated, although disputed in almost every case (see Sinclair and Murawski 1997). These controversies have anchored discussions of recent stock declines. However, the Newfoundland commercial cod fishery spans over 500 years and there has been little attention to and no analyses of previous fishery crises. The goal of this paper is to investigate conflicting arguments about posited effects of overfishing and "natural" productivity change. To do this, I take an historical view and

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ask a simple question using a modelling approach. Can assumptions of constant, random, or depensatory population growth rate and environmental carrying capacity, as inferred by a fishery-only argument, be reconciled with known catches and the historical record of this fishery over 500 years? Alternatively, are assumptions of environmental forcing of productivity consistent with history?

Methods

A surplus production biomass model was employed. The chief parameters of this model are the "intrinsic" rate of population growth (r), the carrying capacity of the ecosystem (K), and the initial biomass. It was assumed that initial biomass was at carrying capacity in 1505. Three sets of assumptions were tested: (1) constant or random r and K; (2) depensation of r; and (3) systematic changes in r driven by a climate index based on tree ring growth. The model took the form

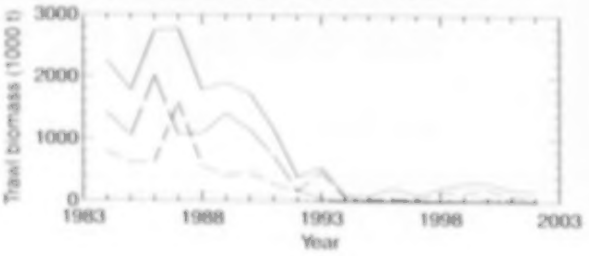
$$B_y = B_{y-1} + rB_{y-1}[1 - (B_{y-1}/K)] - \text{Catch}_{y-1}$$

where B_y is biomass in year y. Under assumption 1, r was either constant or varied at random between 0 and 1. Under assumption 2, r was defined as $[B/(aK + B)]r_b$, so that a base r_b that applied at biomass levels >$K/2$ was increasingly reduced at lower biomass levels. Under assumption 3, r was defined as $r_b p$, where p is a normalized index of climate based on tree ring growth. The combined model defined r as $p[B/(aK + B)]r_b$. Parameter values were determined by iteration using the Solver minimization algorithm in MS Excel to find the best fit with the total survey index (Fig. 1).

Initial fitting of the model to the survey index suggested $r = 0.35$ and $K = 7$ million tonnes (t) ($r^2 = 0.67$). However, reasonable fits could also be obtained with $K = 8$ million t and $r = 0.29$ ($r^2 = 0.40$), $K = 9$ million t and $r = 0.25$ ($r^2 = 0.64$), and $K = 6$ million t and $r = 0.44$ ($r^2 = 0.39$). Current low levels of biomass and the shortness of the fitted survey index relative to the landing data resulted in r being adjusted during iterative fits to the survey index with only minor changes in K if initialized between 6 and 9 million t. All of these combinations of r and K gave very similar biomass trend outputs. Hence, in all subsequent model runs, K was set at 7 million t, which was similar to the total stock abundance determined in an independent study (Robichaud and Rose 2004).

Reconstruction of landings was undertaken by linking records of catches and exports from published sources, the Newfoundland archives, Colonial records, and English, French, Spanish Basque, and Portuguese fishery records, standardized to wet mass equivalents (Fig. 2*a*). Data and sources are available from the author. The tree ring data were obtained from D'Arrigo and Jacoby (1992) for 1600–1974. They represent annual temperatures for northern North America, based on growth chronologies of white spruce (*Picea glauca*) and white cedar (*Thuja occidentalis*), with spatial distribution from Alaska to northeastern Quebec. These data contain both low- and high-frequency climate signals (D'Arrigo and Jacoby 1992). Temperatures for 1975–1998 were obtained from Greenland. The tree ring and Greenland data were strongly correlated over their period of overlap (1871–1967; $r^2 = 0.71$). The cooling event of the early to mid-1800s has been corroborated by other paleoclimatic data (D'Arrigo and Jacoby 1992). Cod survey data were taken from Canada Department of Fisheries and Oceans reports (see Fig. 1).

Fig. 1. Trawl survey mean biomass index (not from population models) for the cod (*Gadus morhua*) stocks around Newfoundland and Labrador from 1983 to 2002 (solid line, total; long-dashed line, northern stock, NAFO Division 2J3KL; short-dashed line, Grand Bank stock, 3NO; dotted line, southern stock, 3Ps). Northern gulf stock (3Pn4RS) is not shown but is included in the total. Data are from stock reports (Brattey et al. 2002; Frechet et al. 2002; Healey et al. 2002; Lilly et al. 2000). t, tonnes.



A quantitative comparison of model outputs with the total survey index for the years 1984 to 2002 and both a quantitative and qualitative comparison with the historical record were used to judge how well outputs mimicked history. For the 19th century, an index of catch per unit effort (CPUE) was derived from landings and human population data from Newfoundland and Labrador (Mannion 1977).

Results and discussion

The model with constant parameters ($r = 0.3534$, $K = 7$ million t) balanced fishing removals until the mid-20th century, indicated a crash in biomass after the 1960s, and reasonable rebuilding in the late 1990s (Fig. 2*d*). Alternative fits with lower r (e.g., 0.25) and higher K values gave similar results. In all cases, model predictions suggested a quicker rebuilding (to approximately 1 million t) than evident in recent survey data and failed to capture any historical variability. Previous attempts to predict population growth of northern cod based on constant parameters are similarly flawed (Myers et al. 1997). Random variation in r and K produced even less realistic outputs (not shown). Climate variation in r forced by the tree ring index suggested a major decline in biomass in the 19th century, but the model output did not correlate with the survey index and predicted an unrealistic increase in biomass in the late 1990s to >1 million t (Fig. 2*d*). Depensatory variation in r captured the decline in biomass in the late 20th century but did not mimic historical variability (not shown). Moreover, the depensatory model resulted in unrealistically low current biomass levels of approximately 75 000 t, as compared with survey (Fig. 1) and biomass estimates using other methods (Lilly et al. 2000; Brattey et al. 2002; Healey et al. 2002; Frechet et al. 2002).

Scaling r by the climate index and a depensation parameter produced an output that correlated strongly with the survey index ($r^2 = 0.80$) and a biomass record consistent with the historical record (Fig. 2*b*). In this formulation (termed the final model), mean r was 0.28 (standard deviation (SD) = 0.09) with a fitted depensation parameter ($a = 0.058$).

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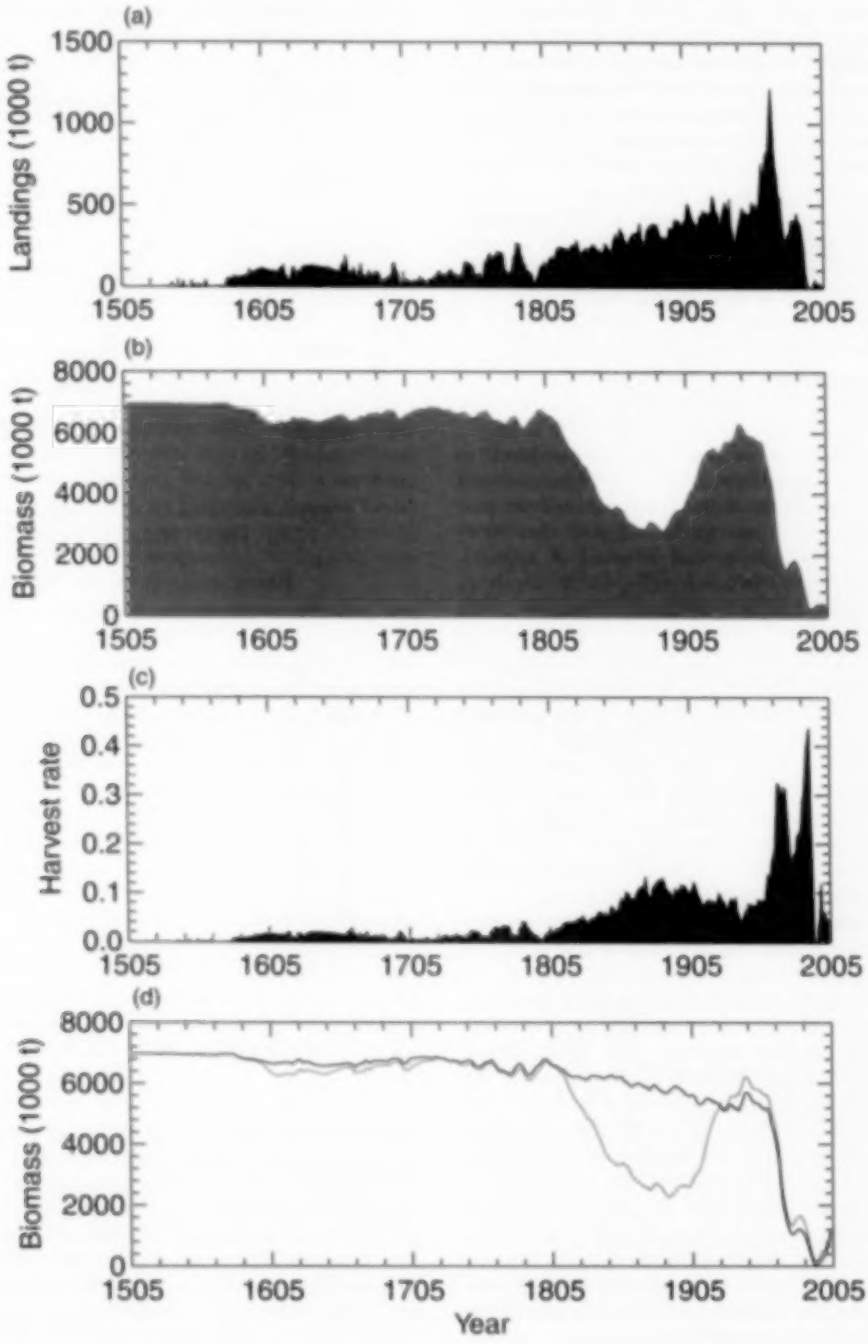
Fig. 2. (*a*) Historical reconstruction of the landings of cod (*Gadus morhua*) in Newfoundland and Labrador waters from 1500 to 2003; (*b*) final surplus production model output for assumptions of combined effects of climate and depensation; (*c*) annual harvest rate (landings per biomass); and (*d*) surplus production model outputs based on constant r and K parameters (blue) and the climate index alone (red).



During the 16th to 18th centuries, the final model suggests that fishing had little impact on the cod stocks. Annual harvest rates were <5% (Fig. 2*c*). However, reductions are predicted to have begun in the 19th century, during the Little Ice Age, as harvest rates exceeded 10% and outstripped declining productivity. Reductions were countered by strong productivity from the early 1900s to about 1960, but by the mid-1960s, fishing removals rose to >30% and greatly ex-

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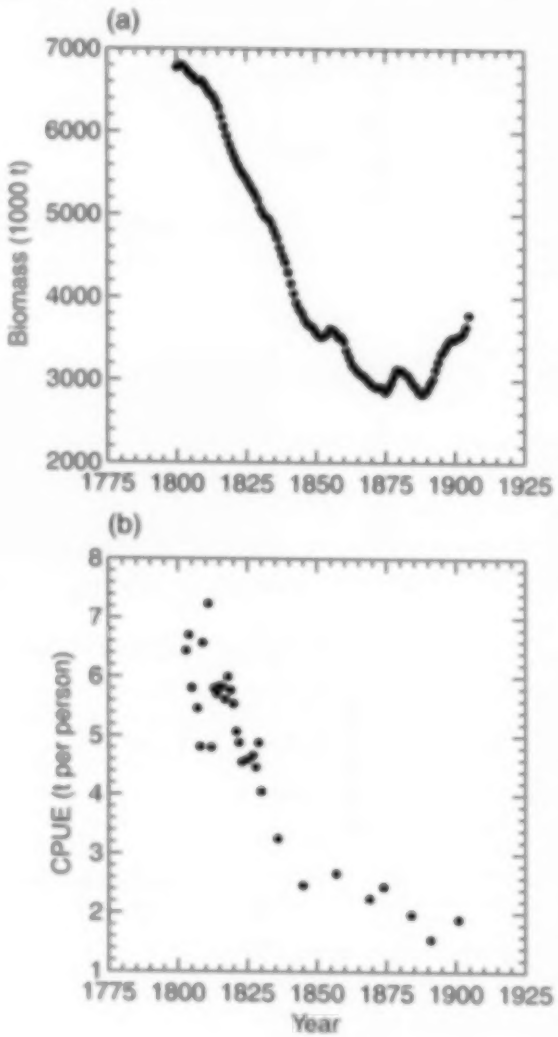
ceeded productivity (equivalent to $F = 0.4$). It would be of interest to compare the harvest rates with estimates using other methods. The longest and arguably most reliable series available is for North Atlantic Fisheries Organisation (NAFO) division 3Ps (Brattey et al. 2002). Levels and trends in annual harvest rates are similar to those determined from virtual population analysis (VPA). For example, final model F of 0.4 in the late 1960s is similar to VPA-determined 0.37 for 1968, ages 4–10 (the fished ages). In the early 1990s, annual harvest rates exceeded 45% (equivalent to $F = 0.6$). For 3Ps, VPA-determined Fs were 0.54 and 0.55 for the same ages for 1991 and 1992, respectively (Brattey et al. 2002). For the other stocks, Fs of the same ages in 1991 and 1992 were 0.59 and 0.90, respectively, in NAFO 3Pn4RS (Frechet et al. 2002) and 0.72 and 0.65, respectively, in NAFO 3NO (Healey et al. 2002). For NAFO 2J3KL, the reliability of VPA Fs is suspect. It is evident that the continuation of high levels of fishing during the period of poorer productivity following the 1960s, compounded by the depensatory effects of recruitment overfishing of a steadily declining biomass, led to catastrophic stock declines from 1970 to 2000.

Biomass was predicted to decline to record low levels in the early 1990s and then show only very slow recovery thereafter, which is consistent with observations of the past decades (Rice 2002). The final model suggests that Newfoundland cod currently have a total biomass of approximately 400 000 t (with poor to no overall growth, largely as a result of depensatory effects), which is comparable with current best estimates. This is a pooled result that does not differentiate among stocks. It is likely that south coast and to a lesser extent northern Gulf of St. Lawrence stocks have grown faster than Grand Bank and northeast Newfoundland and Labrador shelf stocks. An inference from these results is that population growth will only occur when environmental conditions boost productivity above the deficit caused by the lingering effects of recruitment overfishing. At present, there is much evidence of an increased rate of natural mortality in some of the stocks (not in NAFO 3Ps). This is hidden in the depensation term of the final model.

It is not difficult to accept that r and perhaps K have fluctuated historically and declined in the past two decades. Initial attempts were made to isolate changes in r and K, but this proved difficult; hence caution must be used in interpreting one in isolation of the other. Nevertheless, in stocks depressed well below carrying capacity, such as is almost certain in the last half of the 20th century (the period of fit), productivity changes will likely be expressed through r and not K in the model, even if K has in reality changed, which is at least consistent with the formulation of the present model. It is noteworthy that the mean r of the final model is closer to single values determined by stock–recruitment analyses of recent data (e.g., Myers et al. 1997) but, unlike those estimates, does not require a higher K or initial biomass to achieve a good fit with both recent survey and historical fisheries and demographic data. No constant values can fit both the recent and historical data.

Both data and anecdotes can be used to judge the veracity of predicted stock biomass in historical times. The final model predicts steep declines in biomass during the Little Ice Age of the 19th century that correlate strongly with the CPUE index (Fig. 3; $r = 0.95$). Predictions from models that did not include the tree ring index did not correlate with the CPUE index. The CPUE index used here assumes that in the 19th century, "labour in the fishery rose almost in proportion to general population growth until the 1880s" (Mannion 1977). This is likely the only period of Newfoundland history when this assumption is tenable, because before the 19th century, the fishery had a major nonresident component, and after 1880, industrialization and changes in the fishing methods (see Mannion 1977) would invalidate the use of population as a basis for fishing effort. To add support for this interpretation, there are many rich anecdotes of the climate and fisheries of this era based on local knowledge. For example, the seminal "History of Newfoundland" (Prowse 1895) infers from available evidence from fisher-

Fig. 3. For the 19th century, (*a*) cod (*Gadus morhua*) biomass output from the final surplus production model based on variable climate effects and depensation on r and (*b*) an index of catch per unit effort based on landings per population (demographic data from Mannion 1977). The two series are strongly correlated ($r = 0.95$; $p < 0.01$).



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men that cod stocks fared poorly during this cold era, so much so that the preface states of Newfoundland, "her geographical position requires that she should always stand prepared for suffering … if her natural resources are liable to collapse, they are not less liable to sudden and brilliant revival". By 1880, the perceived fishery collapse, based on the CPUE decline, resulted in a cod hatchery being established in an attempt to restock the fish. However, despite stock decline, there is no evidence of sustained and total stock collapse in these earlier times, as has occurred in the late 20th century, and this can be attributed to the vastly differing levels of fishing technology and power between these eras.

In the final decades of the 20th century, there is quantitative evidence of overfishing, stock reductions, and declines in both growth and recruitment in the historically dominant northern cod (50% of total historical biomass) and other stocks (Rice 2002). There is also evidence of climate change (or variability). Ocean conditions in the early 1990s were among the coldest on record in Newfoundland and were accompanied by many changes in both abiotic and biotic conditions in the ecosystem (Drinkwater 2002). Of particular biological relevance, the former chief prey of Newfoundland cod, the capelin (*Mallotus villosus*), has declined in northern areas since 1990, and predation by harp seals has increased (Sinclair and Murawski 1997). The details are of necessity complex, because climatic, oceanographic, biological, and fishery-induced changes are inextricably linked.

In contrast to the complexities of the real ecosystem, the strength (and perhaps weakness) of the present analysis is thought to be its simplicity and that it covers the full duration of the fishery (>500 years). Although I caution against an overly literal interpretation of the parameter values of the model, the results indicate that for cod, the rate of growth and carrying capacity have not remained constant over time. Over the past 500 years, stock declines resulting from both overfishing and climate-induced productivity changes are evident, but the modest fisheries of earlier eras precluded long-term or widespread stock collapse. It is important to note that natural productivity change alone has not collapsed the stocks during this period. The largest reduction before the last half of the 20th century occurred during the Little Ice Age in the mid- to late 19th century and may be attributed to declining productivity with no reduction in the fishery. During the period of decline, catch increased little or not at all, despite a three- to four-fold increase in settlement (and fishing effort).

Also, according to the present analyses, the major collapses of the 1960s were caused entirely by fishing (this was the era of burgeoning fleets of European factory trawlers) during a time of relatively high productivity. Unfortunately, the false assumption that such levels of productivity would continue underpinned fisheries management policy. The Kirby report[1] of the Canadian government that guided policy stated: "Although the industry has many problems, a shortage of fish is not one of them". The effects of recruitment overfishing and declining productivity were not foreseen. In conclusion, it is necessary to take overfishing, climate, and depensation into account to explain both the history and the current state of the cod stocks of the northwest Atlantic.

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[1] A 1982 report entitled "Navigating troubled waters: a new policy for Atlantic fisheries", available from the Ministry of Supply and Services, Ottawa, Ontario.

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Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*)

K. Brander and R. Mohn

Abstract: We examine the effect of introducing an environmental factor — the North Atlantic Oscillation (NAO) index — into a stock–recruit relationship fitted to 13 North Atlantic cod (*Gadus morhua*) stocks and discuss the implications for management. The NAO has a significant effect on recruitment of four of the stocks (positive effect on recruitment in the North Sea, Baltic Sea, and Irish Sea; negative effect on recruitment at Iceland), and the pattern of positive and negative effects on all stocks is consistent with the geographic influence of the NAO on environmental variables. Observed variability in the NAO should be taken into account in interpreting the causes of past changes in cod stocks. The NAO index for the previous winter is available by April and thus may provide an early indication of the likely range of cod recruitment in the current year. In areas, such as the North Sea, where the effect is strong, medium- and long-term assessments of recruitment and yield of the cod stocks should consider likely future states of the NAO. The NAO can be used to represent environmental variability in stock projections and thereby provide a better basis for the estimation of risk.

Résumé : Nous examinons les effets de l'introduction d'un facteur du milieu, l'indice de l'oscillation nord-atlantique (NAO), dans une relation stock–recrutement ajustée à 13 stocks de morues (*Gadus morhua*) de l'Atlantique nord et nous discutons des implications sur les avis de gestion. NAO a un effet significatif sur le recrutement de quatre des stocks (un effet positif sur les stocks de la mer du Nord, de la Baltique et de la mer d'Irlande et un effet négatif sur le recrutement en Islande); le pattern d'effets positifs et négatifs sur tous les stocks est en accord avec l'influence géographique de NAO sur les variables environnementales. On devrait tenir compte de la variabilité observée de NAO pour interpéter les changements du passé dans les stocks de morues. L'indice NAO pour l'hiver précédent est disponible en avril et peut donc fournir une première indication de l'entendue vraisemblable du recrutement de la morue durant l'année courante. Dans les endroits, comme la mer du Nord, où l'effet est important, l'évaluation à moyen et à long termes du recrutement et du rendement des stocks de morues devrait tenir compte des états futurs vraisemblables de NAO. NAO peut servir à représenter la variabilité de l'environnement dans les projections de stocks et ainsi fournir une base plus solide pour l'estimation des risques.

[Traduit par la Rédaction]

Introduction

Fish recruitment depends on reproductive output (i.e., number of viable eggs, usually represented or approximated by the spawning stock biomass, SSB) and on survival of eggs, larvae, and juveniles (Cushing 1996). Variability in recruitment is the principal cause of fluctuation in fish stocks and, hence, catches (Cushing 1996). One of the goals of medium- and long-term management is to minimize the risk of reduced recruitment. Relationships between SSB and recruitment (stock–recruit relationships) are used to provide advice on how to achieve this (Sissenwine and Shepherd 1987). However, reproductive output, survival rate, and hence recruitment may be affected by environmental factors, which raises the question of whether advice on achieving medium- and long-term goals should also take environmental factors into account?

A number of studies have demonstrated that interannual variability in temperature affects survival and recruitment of cod (*Gadus morhua*), with positive effects at the cold end of the species range and negative effects at the warm end (Ottersen et al. 1994; Planque and Fredou 1999; Brander 2000). Survival and recruitment are influenced by many factors in addition to temperature; for example, in the Baltic Sea a combination of extreme conditions of salinity (density) and oxygen has a profound effect on egg survival (Koester et al. 2001). Food availability for rapidly growing larvae affects their survival in many if not all areas. The 90-year-old match–mismatch hypothesis, which relates survival of fish larvae to the timing and quantity of suitable food, continues to be tested, using a combination of modelling, remote sensing, and field observation (Brander et al. 2001; Beaugrand et al. 2003).

Despite extensive experimental and field studies it has proved difficult to determine which processes consistently exert a major influence on recruitment, and when they occur during early life. Consequently the appropriate location and

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Table 1. Time series and source of cod stock and recruitment data used in the analysis.

Stock	First year	Last year	No. of years	Recruit age	Reference
Celtic Sea	1971	2000	30	1	ICES 2002
Baltic Sea	1966	1999	34	2	ICES 2002
Faroes	1961	1999	39	2	ICES 2002
Iceland	1955	1998	44	3	ICES 2002
Irish Sea	1968	2000	33	0	ICES 2002
Northeast Arctic	1946	1998	53	3	ICES 2002
North Sea	1963	2000	38	1	ICES 2002
Western Baltic Sea	1970	2000	31	1	ICES 2002
Western Scotland	1966	1999	34	1	ICES 2002
NAFO 4VsW	1970	1994	25	1	Mohn et al. 1998
NAFO 4X	1983	2001	19	2	Clark et al. 2002
Georges Bank	1979	2000	22	1	O'Brien and Monroe 2001
NAFO 2J3KL	1962	1986	25	3	Lilly et al. 2001

Note: NAFO, North Atlantic Fisheries Organization.

season at which environmental factors such as temperature should be measured remain uncertain. Process uncertainty entails measurement uncertainty, thus there will be imprecision in estimating the appropriate values of environmental variables, even when complete and detailed observations are available. The problem is mitigated to the degree that the signal of interannual variability in environmental factors extends across time and space scales, but the selection of environmental variables and their measurement remain, to a greater or lesser extent, empirical.

The problem of how to select the appropriate location and season to represent interannual variability in the environment does not arise when a climate indicator such as the North Atlantic Oscillation (NAO) is used, since it does not have local values. The winter (December–March inclusive) state of the NAO is an indicator of interannual climate variability over the North Atlantic and northwest European shelf seas (Hurrell et al. 2003). It influences, and can be used as a proxy for, temperature, wind, and precipitation during the following spring. Ottersen et al. (2001) provide examples of a range of direct and indirect ecological effects of the NAO on terrestrial and marine biota.

Direct and indirect mechanisms of the kind identified by Ottersen et al. (2001) probably account for the effects of the NAO on cod recruitment, but these may not be the same for all stocks and time periods. Thus the driver (the NAO) is precisely defined, but the processes by which it acts are vague.

Changes in the state of the NAO are being investigated as part of global-climate modelling and seem to be related to changes in deep convection and the thermohaline circulation (Meincke et al. 2003). This suggests that decadal changes in the North Atlantic need to be considered as coupled processes and that time series of the relevant parameters can be expected to provide a degree of predictive potential.

It is useful to evaluate the consequences of changes in the NAO for cod stocks in order to improve our understanding of the causes of past variability and indicate how information about future climate scenarios may be used to improve management advice. A notable example of past variability is the "gadoid outburst" in the North Sea, which occurred in the period from the early 1960s to mid-1980s, when recruitment and catches of the four main gadoid species increased to much higher levels than had previously occurred (International Council for the Exploration of the Sea (ICES) 2001). It is also useful to relate the effects of the NAO on cod to its effects on other components of marine and terrestrial ecosystems.

Material and methods

Cod stock and recruit data were compiled by means of population reconstruction (using virtual population analysis, VPA) based on catches in commercial fisheries and research surveys for nine northeast Atlantic and four northwest Atlantic stocks (data sources are shown in Table 1). The number of years available for the analysis of each stock ranged from 19 to 53 and averaged 30. Data on weight, maturity, and fishing and natural mortality at age for North Sea cod (ICES 2003) were used in a production model to estimate the equilibrium yield.

The NAO time series (Fig. 1) is the winter (December–March) mean pressure difference between southwest Iceland and Gibraltar (Jones et al. 1997). This series is used for comparability with the study of ecological effects by (Ottersen et al. 2001). The degree of similarity between this series and the alternative index, which uses data from Lisbon, can be judged from the coefficient of determination (r^2), which is 0.91 for the period 1864–2002.

The NAO influences sea-surface temperature (SST), winds, storm tracks, and precipitation over the North Atlantic (Hurrell et al. 2003). An example is the geographic pattern of the effect of the winter NAO index on SST in the following spring (March–May) as shown by a seasonal correlation between them obtained from the National Oceanic and Atmospheric Administration Cooperative Institute for Research in Environmental Sciences Climate Diagnostics Center (Fig. 2).

The standard Ricker function (Ricker 1954) relating stock (SSB) to recruitment, R, is expressed as

$$(1) \qquad R = a\,\mathrm{SSB}\exp(-b\,\mathrm{SSB})$$

The parameters can be redefined in more natural units using the curve's maximum point, SSB_{max}, R_{max}.

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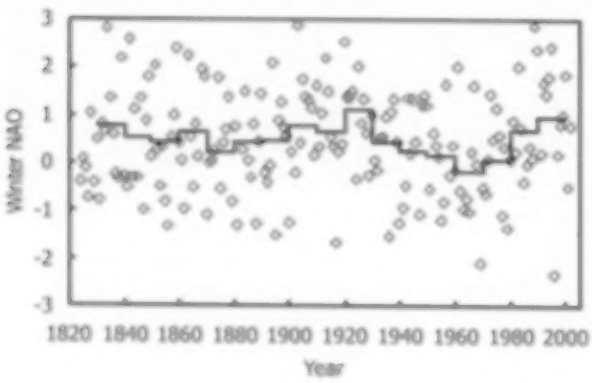
Fig. 1. Winter (December–March inclusive) values of the North Atlantic Oscillation (NAO) calculated from southwest Iceland to Gibraltar (Jones et al. 1997), showing annual values (◇) and decadal means (solid line).



$$R = \exp(R_{max}/\mathrm{SSB}_{max})\,\mathrm{SSB}\,\exp(-\mathrm{SSB}/\mathrm{SSB}_{max}) \quad (2)$$

This parameterization allows a direct interpretation of the parameters. It was then given a third, environmental parameter, which is the coefficient of the NAO:

$$R = \exp(R_{max}/\mathrm{SSB}_{max})\,\mathrm{SSB} \times \exp(-\mathrm{SSB}/\mathrm{SSB}_{max})\exp(c\,\mathrm{NAO}) \quad (3)$$

Equations 2 (two-parameter model) and 3 (three-parameter model) were fitted to the data using a Markov Chain Monte Carlo algorithm. A recent nontechnical review of this algorithm and its uses appears in Harwood and Stokes (2003). Although this method can use prior information about the expected parameter values, none was used for this analysis. The best solution in terms of log likelihood after 10 000 steps was chosen. This approach was taken so that the distribution of probable parameter values could be explored. We summarize the results and include the parameters from the two- and three-parameter fits (Table 2).

The Akaike Information Criterion (AIC; Akaike 1974) was used to statistically compare the two- and three-parameter fits. A lower AIC value corresponds to a better model fit. The AIC compares the negative log likelihoods of the two models with a penalty for a greater number of parameters. The addition of a parameter is considered to have significantly improved the model fit if the AIC is reduced by more than 2 (Burnham and Anderson 2003). We present the AIC for the two- and three-parameter models as well as its change (Table 2).

To assess the potential impacts of the NAO on management metrics a production model (Sissenwine and Shepherd 1987) was applied. This model was chosen because it directly links the stock–recruit information (as well as weight-at-age, partial-recruitment, and age at maturity data from ICES 2003) to the estimation of equilibrium yields. As an illustration, equilibrium yield and the associated SSB and recruitment were estimated for North Sea cod, using the appropriate coefficients for the three-parameter model (Table 2).

Results

For four stocks (North Sea, Baltic Sea, Iceland, and Irish Sea) the AIC decreased by more than 2 as a result of adding the NAO parameter, indicating that the fits were significantly improved. Although there is little difference between the two- and three-parameter fits for North Sea cod when the mean NAO value is used (Fig. 3), the effect of using the 10th and 90th percentiles of the NAO is substantial (Fig. 4). The 10th percentile (–1.1) results in recruitment of North Sea cod, which is 77% greater than the 90th percentile (+2.0). During the 1990s the average value of the NAO was high (+0.96, see Fig. 1), with two years (1990 and 1995) above the 90th percentile and one year below the 10th percentile (1996, the highest cod recruitment of the decade). The same percentiles are used to show how the relationships between fishing mortality and equilibrium yield and recruitment are affected by varying levels of the NAO (Fig. 5). The fishing mortality that produces the highest equilibrium yield drops from 0.84 (for NAO = –1.1) to 0.6 (for NAO = +2.0). For recruitment the equivalent levels of fishing mortality are 0.95–0.66.

One of the aspects of the chosen fitting procedure is that it allows an investigation of the parameter space used in the model and a better understanding of process error. Because the Ricker parameters were transformed into more natural units, relative to SSB_{max} and R_{max}, the stock and recruit data may be plotted on the same axes. For example, a plot of SSB_{max} and R_{max} for North Sea cod shows that they are highly correlated (Fig. 6*a*). The contour of the 50th percentile of these parameters lies mostly outside the range of observed data. This is commonly observed with stock and recruit data, and suggests that the curvature of the relationship is not well supported in the data, probably because the dynamic range of the data is insufficient to produce a good fit for this model. The NAO parameter (Fig. 6*b*) is well behaved and independent of SSB_{max}. For three of the stocks shown in Table 2 (Georges Bank, Celtic Sea, and NAFO 2J3KL) the values of SSB_{max} and R_{max} in the two- and three-parameter fits are very different. This probably arises because the likelihood surfaces are long flat valleys and the location of maxima within the valleys can be greatly perturbed when the NAO is included.

The geographic pattern of the effects of the NAO on recruitment can be compared with the geographic pattern of the effects of the NAO on SST (Fig. 2). Strongly negative coefficients for the relationship between NAO and recruitment occur in the North Sea, Baltic Sea, and Irish Sea, where the relationship between NAO and SST is strongly positive. In the western Atlantic Ocean, Georges Bank and the Eastern Scotian Shelf also have negative coefficients relating NAO and recruitment. Two positive coefficients for the relationship between NAO and recruitment (Iceland and 2J3KL) occur where the relationship between NAO and SST is negative. The coefficients for other stocks (northeast Arctic, Faroes, Celtic Sea, and Western Scotian Shelf) are close to zero.

Discussion

All the stock and recruit information in this study came from VPA, but the approach could also be applied to stocks

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Fig. 2. Contours of the seasonal correlation between winter North Atlantic Oscillation (NAO) and sea-surface temperature (SST) from March to May 1948–2000. SST values are from a reanalysis by the US National Center for Atmospheric Research of the US National Centers for Environmental Prediction, courtesy of the National Oceanic and Atmospheric Administration Cooperative Institute for Research in Environmental Sciences Climate Diagnostic Center. The symbols (+, 0, -) indicate the sign of the relationship between NAO and cod (*Gadus morhua*) recruitment in the three-parameter Ricker model. The size of the symbols indicates the strength of the relationship.

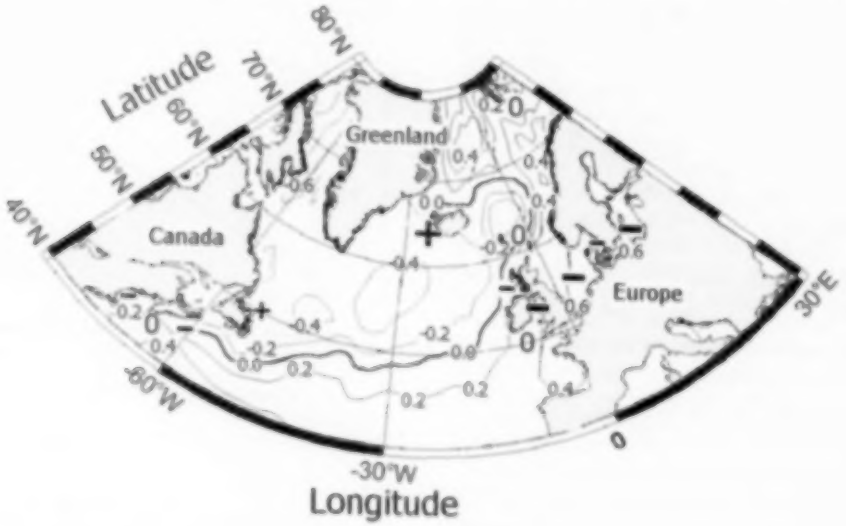

Table 2. Two- and three-parameter model fits and increment in the Akaike Information Criterion (AIC) between the models.

Stock	Two-parameter model			Three-parameter model					
	SSB_{max}	R_{max}	AIC2	SSB_{max}	R_{max}	NAO	AIC3	ΔAIC	No. of years
North Sea	371.5	461.7	64.7	257.1	414.2	–0.195	60.3	4.4*	38
Baltic Sea	744.2	371.7	59.6	693.9	384.8	–0.181	55.9	3.7*	34
Iceland	794.4	224.7	45.5	892.1	228.3	0.109	43.0	2.5*	44
Irish Sea	18.1	6.9	61.5	16.3	7.2	–0.177	59.0	2.5*	33
Western Baltic Sea	74.0	85.3	63.0	53.8	83.6	–0.183	61.5	1.5	31
NAFO 4VsW	158.9	115.6	34.5	137.3	123.9	–0.163	33.2	1.3	25
Western Scotland	34.7	9.4	55.9	33.1	9.7	–0.118	55.5	0.4	34
Georges Bank	34 624.0	2909.0	41.7	1 452.9	140.0	–0.151	41.6	0.1	22
Northeast Arctic	720.7	710.2	100.3	714.1	704.1	0.023	102.1	–1.8	53
Celtic Sea	91.2	12.3	70.1	346.1	43.7	–0.056	72.0	–1.9	30
Faroes	45.9	17.5	70.8	45.8	17.3	0.007	72.8	–2.0	39
NAFO 4X	110.7	22.4	26.2	117.3	23.4	–0.021	28.2	–2.0	19
NAFO 2J3KL	2 899.3	703.5	42.2	18 355.9	3601.5	0.078	45.6	–3.4	25

Note: SSB, spawning stock biomass; *R*, recruitment; NAO, North Atlantic Oscillation; NAFO, North Atlantic Fisheries Organization.
*Value is statistically significant.

for which this analysis is lacking, possibly because full catch-at-age data are not available. Population reconstruction from VPA smooths the data, giving better fits to the stock–recruit model, but it requires estimates of natural mortality. If these are correct, especially with regard to changes over time, then estimates of stock and recruitment from VPA or fishing surveys should be equally sensitive to changes in the NAO, although the underlying shape may be different. Extension of our analysis to stocks with data on abundance-at-age, but no formal assessment, would also be possible. Numbers at age from survey data, or catch-per-unit-effort, could also have been used either directly or corrected for changes in catchability. Even if the abundance data were size-disaggregated, but not aged, it would be possible to investigate the influence of the NAO on reproduction. An estimate of recruitment could be made using the number of individuals within a specified (juvenile) size range, and SSB could be estimated using the numbers above a size threshold, which approximates the size at 50% reproduction, with a correction for allometric relationships.

The effects of climate variability on cod recruitment are well known (Dippner and Ottersen 2001; Koester et al. 2001), as is the correlation between recruitment of adjacent stocks (Myers et al. 1995; Brander 2003). The decorrelation scale for cod recruitment in the North Atlantic has been estimated as less than 500 km (Myers et al. 1995). However, the

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Fig. 3. Stock–recruit data for North Sea cod for 1963–2000 and relationships fitted using two-parameter (dotted line) and three-parameter (solid line) Ricker models. The average NAO for the period 1963–2000 (+0.41) was used in the three-parameter fit.

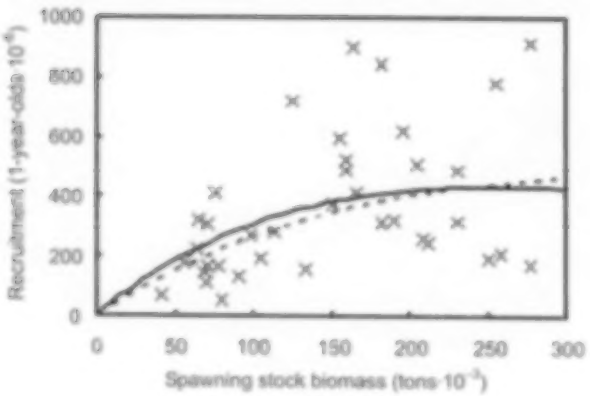
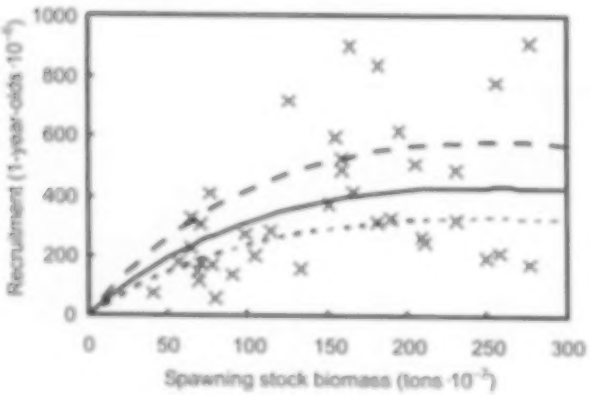


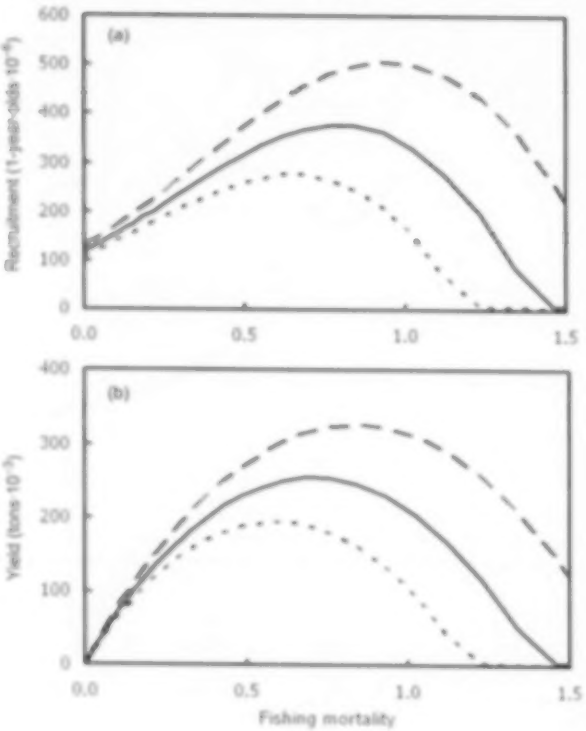
Fig. 4. Three-parameter Ricker model for the North Sea cod with NAO values set at average (+0.41, solid line), 10th percentile (–1.1, broken line), and 90th percentile (+2.0, dotted line) for the period 1963–2000.



comparison of NAO effects on temperature and on recruitment suggests that the pattern of correlations is probably anisotropic and is a result of the geographic pattern of the environmental forcing. Interannual climate variability, as represented by the NAO, probably affects all cod stocks of the North Atlantic, but the magnitude and sign of the effect vary, because the influence of the NAO on the underlying physical factors, including temperature, windspeed, and cloud cover is not geographically uniform.

Published relationships between temperature and recruitment (Planque and Fredou 1999; Brander 2000; O'Brien et al. 2000) provide an alternative way to introduce environmental information into stock–recruit relationships and to explore short- and long-term implications. However, these relationships, which are mainly empirical but include some information from process studies, illustrate how difficult this is in practice. For example, Planque and Fredou (1999) analysed the spatial and temporal variability of temperature to

Fig. 5. Recruitment (*a*) and equilibrium yield (*b*) for the North Sea cod, using the Sissenwine–Shepherd production model (Sissenwine and Shepherd 1987) and the three-parameter stock–recruit model with NAO values set at average (+0.41, solid line), 10th percentile (–1.1, broken line), and 90th percentile (+2.0, dotted line) for the period 1963–2000. Fishing mortality is the unweighted mean over the exploited ages.



justify the use of a value that was averaged over a large region. They found a significant correlation between annual temperatures for north and south Iceland and used a value that combined the two regions. Brander (2000), on the other hand, used temperatures for the specific area off southwest Iceland where cod larvae are, on average, most abundant during weeks 14–26. Both authors then found significant temperature–recruitment relationships for Iceland cod, but Planque and Fredou (1999) obtained a positive relationship (i.e., higher temperature results in higher recruitment) and Brander (2000) a negative relationship. The difference probably arises as a result of the inclusion of temperature data from north of Iceland by Planque and Fredou (1999). Although they showed that temperatures north and south of Iceland are significantly correlated, the relationship accounts for less than 50% of the total variance. The effects of temperature on growth and survival of cod larvae have been studied experimentally (e.g., Otterlei et al. 1999), and the processes by which temperature affects recruitment are being identified and quantified. This should result in more precise specification of where and when to measure effective ambient temperature in the field.

Cod recruit data are available for the past four or five decades. During this period the NAO has swung from the low-

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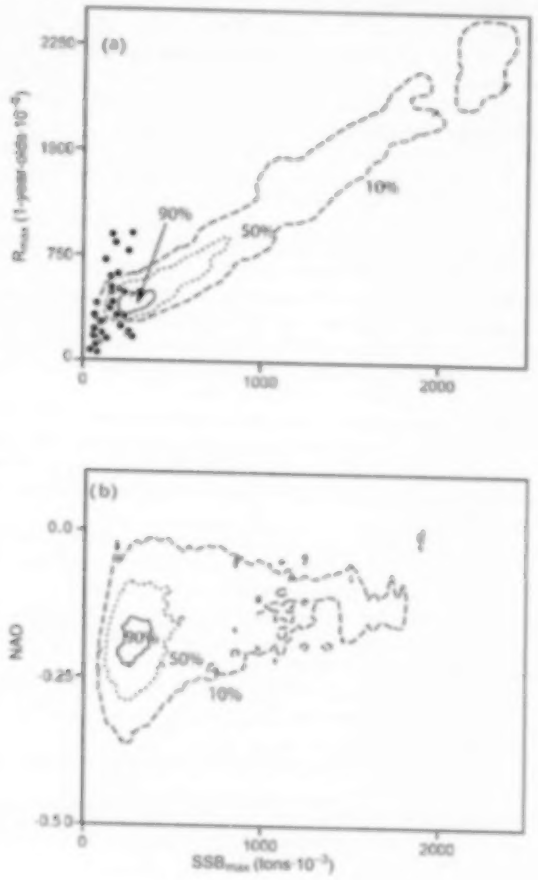
Fig. 6. Two-dimensional plots of the likelihood surfaces for the parameters of the three-parameter model using recruitment (*a*) and NAO (*b*) data for the North Sea cod. The contours are the 10th, 50th, and 90th percentiles. For reference, the stock and recruit data are plotted in *a*.



est decadal means in the 179-year observational record (during the 1960s and 1970s) to the second highest decadal mean (during the 1990s). Based on the analysis presented here, the increase in the NAO since the 1960s probably had a significant negative effect on cod recruitment in the Irish Sea, North Sea, and eastern Baltic Sea and a positive effect at Iceland. These findings are all consistent with a positive relationship between temperature and recruitment; however, the analysis does not allow us to conclude that temperature is the only factor or that the same processes are acting in each area.

Should information about the NAO influence advice on medium- and long-term management? If one accepts the evidence that the NAO (or environmental factors influenced by it) affects recruitment, then an assumption about its future state is necessary, irrespective of whether this can be predicted. The implicit assumption when using the two-parameter Ricker stock–recruit relationships is that future values of the NAO will be like those that generated the recruitments observed during the time period of the data, i.e., stationary. For most stocks this includes the two decades (1960s and 1970s) of extreme low values, whereas the mean for the most recent decade (1990s) was the second highest in the instrumental record.

It is not evident that future states of the NAO can be predicted, but it would seem sensible to seek the opinion of climatologists on its likely future state and to include this information in the evaluation of medium- and long-term management options for those stocks on which it can be shown to have an effect. For example, expected yield and recruitment of North Sea cod as a function of fishing mortality are substantially different under high and low NAO regimes. The trend of increasing NAO since the 1960s has probably been a factor in the decline in that stock and in the systematic overassessment of its recruitment potential.

Improving the short-term prediction of recruitment using the NAO index is, of course, also of interest. Our analysis shows that, for a number of stocks, the likely range of recruitment values is affected by the NAO index during the previous winter. We note that the winter NAO index, which is required for the three-parameter model, is available via the web, at no cost, at the same time of year (April) that the early life stages, whose survival the NAO may influence, are in the plankton.

Timely availability and cost are clearly advantages when deciding which environmental variables to use in fisheries models. Other advantages of the NAO are that it features prominently in research on climatology and on the effects of climate change, and that it does not have local values, obviating the need to select a particular value. The disadvantage of using such an indicator is that the mechanisms by which it acts are not clearly identified. There is a trade-off between easy measurement and vague process. However, until we have reliably identified the direct effects of environmental factors and the processes by which they act on recruitment, the NAO may provide a useful "high-level" indicator of interannual variability.

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Assessing food-web structure, matter fluxes, and system attributes of a Central European mountain stream by performing mass-balanced network analysis

Elisabeth I. Meyer and Rainer Poepperl

Abstract: Trophic interactions and cycling of matter within the community in a soft-water mountain stream were analyzed on the basis of a compartment food-web model. The model describes (*i*) the structure of the food web, quantifying biomass, production, and consumption of individual elements as well as of the entire system, and (*ii*) the flow of matter between compartments as well as trophic levels. Detritus and primary producers sustain a broad variety of invertebrate consumers. Fishes are the top predators; sculpin (*Cottus gobio*) and a compartment consisting of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are at the highest trophic level. Heterotrophic microorganisms (227.1 g dry mass (DW)·m^{-2}·year^{-1}) and aufwuchs algae (150.1 g DW·m^{-2}·year^{-1}) have the highest production. Secondary production of fishes and macroinvertebrates amounts to 2.56 and 19.9 g DW·m^{-2}·year^{-1}, respectively. Total consumption amounts to 1136.41 g DW·m^{-2}·year^{-1}. Main flows occur between the lower trophic levels. Food intake is greatest for microorganisms and Ephemeroptera. A relatively high fraction of invertebrate production is consumed by predators. For 10 of 19 compartments, over 95% of production is used as food by other organisms. Transfer efficiencies are generally low (<10%). A large proportion of matter transfer occurs at the lower discrete trophic levels of the stream.

Résumé : Nous avons analysé les interactions trophiques et le cycle de la matière d'une communauté de ruisseau à partir d'un modèle des compartiments du réseau trophique. Ce modèle décrit (*i*) la structure du réseau trophique, en quantifiant la biomasse, la production et la consommation de certains éléments ainsi que de l'ensemble du système, et (*ii*) le flux de matière entre compartiments et entre niveaux trophiques. Nous avons déterminé que le détritus et les producteurs primaires servent de nourriture à une grande variété d'invertebrés consommateurs. Les prédateurs sont les poissons; *Cottus gobio* et un compartiment composé des truites de rivière (*Salmo trutta*) et arc-en-ciel (*Oncorhynchus mykiss*) ont le niveau trophique le plus élevé. Les plus hautes valeurs de production ont été trouvées chez les microorganismes (227,1 g·m^{-2}·an^{-1} poids sec (PS)) et le périphyton (150,1 g·m^{-2}·an^{-1} PS). La production sécondaire des poissons et des macroinvertébrés se monte à 2,56 et 19,9 g·m^{-2}·an^{-1} PS, respectivement. La consommation totale se monte à 1136,41 g·m^{-2}·an^{-1} PS. L'ingestion de nourriture est surtout le fait des microorganismes et des ephéméroptères. Les prédateurs prélèvent une fraction relativement élevée de la production des invertébrés. Dans 10 des 19 compartiments, plus de 95 % de la production sert de nourriture à d'autres organismes. Les taux d'efficacité de transfert sont généralement bas (<10 %). Les flux les plus importants relient les niveaux trophiques discrets inférieurs de ruisseau.

Introduction

Concerning lotic food webs, generally Two types of lotic food web are generally distinguished (Benke and Wallace 1997): the so-called connectivity food web, which is based merely on trophic relationships between species or food resources and consumers, and the quantitative food web. While the connectivity web — also called the binary web, as it considers the presence or absence of a feeding link (Gaedke 1995) — does not take into account the relative importance of food components consumed by a species (Townsend et al. 1998), the latter does. To construct quantitative webs, information on pool size, process rates (e.g., production, respiration, etc.), and diet composition is essential (Polovina 1984; Ulanowicz 1986; Christensen and Pauly 1992*b*). Measurements or estimates of these parameters are a prerequisite for assessing energy flow and hence for understanding the food web (Cohen et al. 1993; Polis 1994).

An intermediate type between connectivity webs and quantitative webs is illustrated by the web developed by Tavares-Cromar and Williams (1996). It categorizes consumers into three feeding types — basal, intermediate, and top species — thus yielding an estimate of "interaction strength" between web components, in this case single species. A further improvement, however, emphasizing only the feeding

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relationships of Trichoptera, has been made by Benke and Wallace (1997). They not only quantified the different food resources used by single species, but also gave estimates of annual production as well as ingestion of each species, thus providing a model of energy flow in the web. Hall et al. (2000) used this method to estimate food-web flows, fractional trophic levels, and other network measures for the entire invertebrate and microbial assemblage of two streams.

Using the fact that ecosystem components are connected in ecological networks (e.g., Pahl-Wostl 1995), a promising approach, which has been applied in marine and pelagic systems (e.g., Gaedke et al. 1996; Carrer and Opitz 1999; Moreau et al. 2001) and recently in stream ecosystems (Poepperl 2003), applies techniques derived from network analysis. To facilitate such procedures, assembly of single species into specific "compartments", i.e., aggregations, and hence data reduction, is required (e.g., Hall and Rafaelli 1991; Opitz 1996). Although on the one hand this implies loss of information (e.g., concerning the "real" linkages between single species), on the other hand it can be assumed that — as has been already shown for pelagic webs (e.g., Gaedke et al. 1996), a littoral community (R. Poepperl and S. Opitz, unpublished data), and a lowland stream (Poepperl 2003) — the emerging mass-balanced flow diagrams considerably enhance knowledge concerning the main pathways and magnitudes of matter and energy fluxes in the system. The principle is that all organisms are allocated to one of a number of compartments, which are interconnected by fluxes of matter. This means that the quantitative importance of the individual flows between the compartments or aggregations is considered, and fluxes to and from the pool of dead organic matter are included. To estimate the magnitude of these fluxes, estimates of the rates of major processes are required for each living compartment (Gaedke 1995).

We applied this approach to a stream ecosystem for which a broad database has been established over the years, allowing mass-balanced network analysis (Christensen and Pauly 1992*a*, 1993*b*; Mavuti et al. 1996). The Steina is a softwater mountain stream in southern Germany that has been studied for nearly a decade from the mid-1980s, with the aim of gaining insight into different ecosystem properties and revealing functional relationships. Therefore, we have quantitative data on ecosystem structure and function (see below). In our model, data required as input variables for all living groups were compartment biomass or abundance and individual biomass, secondary production or the ratio of production to biomass (P/B), and the ratio of production to consumption (P/Q). In addition, biomass and import of detritus, the amount of matter exported from the system by migration (i.e., emerged biomass), an estimate of the percentage of unassimilated food, and diet composition were used as inputs for each ecological group.

Along with the general objective of gaining a better understanding of the structure and functioning of the community by quantitatively describing how matter propagates along pathways of the Steina network, the model had the following more specific aims: (*i*) to provide information on resource utilization and the position of single ecological groups in the trophic web by quantifying consumption, number of predators, and amount of production consumed by predators; (*ii*) to assess the importance of ecological groups in the cycling of matter, such as primary producers, detritus, invertebrates, and fishes; (*iii*) to estimate the size and efficiency of flows between trophic levels with respect to origin or destination; and (*iv*) to provide estimates of biotic parameters not measured in situ by extrapolation from model results. Furthermore, for the purposes of quantitative characterization and classification of the overall system, the model provides system parameters and ratios as well as indicators of system performance and developmental stage according to Odum (1971).

Materials and methods

Study stream

We studied the Steina, a softwater mountain stream in the southern Black Forest of Germany (8°19′E, 47°47′N). The main study section is approximately 10 km downstream of the source and about 720 m above sea level. Because of little land use in the catchment area and of geochemical characteristics, relatively low nutrient levels were measured by Meyer et al. (1990). The stream has low conductivity and moderate discharge, the mean annual discharge ranging from 0.4 to 1.1 $m^3 \cdot s^{-1}$. Stream width varies between 4 and 6.5 m and the stream bed consists mainly of gravel and stones (Mutz 1989).

Field investigations and data collection

Besides a general physicochemical characterization (Meyer et al. 1990), identification and quantification of as many of the system components as possible was performed from 1985 to 1994. Special emphasis was laid on the invertebrate assemblage, for which taxonomic structure, abundances, biomasses, and production have been estimated (Meyer 1991, 1992; Meyer and Poepperl 2003). Other data we used were periphyton (aufwuchs algae) biomass and primary production (Ruhrmann 1990), input and processing of particulate organic matter (Gessner and Schwoerbel 1989; Gessner et al. 1991), and hyporheic respiration (Pusch and Schwoerbel 1994; Fischer et al. 1996). Furthermore, estimates of fish abundance, biomass, and predation pressure on benthic macroinvertebrates could be derived from various field and laboratory experiments (Meyer 1992).

In the following section the most important sampling methods are described in detail. If data from other research scientists working at the Steina were used, a short reference to the method is given in the description of the compartments aggregated for modelling (see below). Since we realized that individual gaps in available data may make it difficult to parameterize a steady-state model as presented in this paper, additional values were taken from the literature. In these cases the origin of the values is described in the section "Network analysis".

Invertebrate biomass and production

Invertebrate sampling was conducted over a 3-year time span from November 1985 to October 1988. Four to seven Surber samples (sampling unit 0.12 m^2, mesh size 300 µm) were taken from different habitat types (riffle, run, stream bank) according to a stratified random sampling regime (Elliott 1983) at 4- to 6-week intervals, resulting in a series of 37 field excursions. Samples were transported individually to the laboratory in thermos bottles, and further process-

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ing comprised sieving into two size fractions, subsampling of the smaller fraction (Meyer 1990), subsequent live-sorting to the lowest possible taxon, followed by dry-mass estimations, or first deep-freezing and later identification and biomass measurements. In the third study year, invertebrates were preserved in 70% ethanol only, and dry mass was determined from conversions of body size to dry mass (Meyer 1989; Wenzel et al. 1990). Invertebrate abundance and biomass were estimated for an average square metre of the stream by considering the proportional areal contribution of the different channel units (riffle, run, stream margin) from which the samples had been taken. A detailed description of the whole sampling and processing procedure is given in Meyer (1991).

Secondary production of invertebrates was estimated using the increment-summation method on those species for which cohorts could be distinguished. For all other species or higher taxonomic assemblages, either averages of published *P/B* ratios were used or, conservatively, a turnover ratio of 5 or 10, as recommended in the literature (Waters 1977; Benke 1996; Meyer and Poepperl 2003).

Fish biomass, consumption, and diet composition

To get information on fish species present, densities, and biomasses, repeated electrofishing runs were conducted on six dates within a time span of 2 years (1986–1988). Catches and biomasses (g wet mass) of fish species that occurred (brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), and sculpin (*Cottus gobio*)) were measured and extrapolated to give density and biomass per square metre. Fish dry mass was calculated assuming that dry mass = 25% of wet mass.

Analysis of ingested food was carried out by gentle stomach flushing of live fish caught in the field (i.e., Gelwick and Mathews 1996) on 21 January and 31 August 1988 (*C. gobio*) and 22 September 1989 and in July and September 1990 (*S. trutta*). For details of the procedure, estimation of flushing success, and daily ratio see Meyer (1992). Dry mass of ingested food was estimated by converting length to mass (Meyer 1989). In organisms where no regression calculations of mass on length were possible, regression formulae for invertebrates with similar shapes were used.

For extrapolation from the daily ration to an estimate for yearly consumption, a multiplier of 255 was used for *C. gobio* (Orsag and Zelinka 1974). To obtain the multiplier for both trout species, the suggestions in Elliott (1972, 1975*a*, 1975*b*) were followed. Hence, it was considered that the number of "gastric evacuations" per day depends on water temperature. The number of complete gastric evacuations per month was determined by multiplying the monthly mean water temperature by the time needed for one evacuation. Summing up these values resulted in a multiplier of 290. Details are given in Meyer (1992).

Network analysis

Modelling approach

The modelling approach used in the present study assumes mass balance, i.e., it balances the flow to and from each ecological group or compartment in the model based on eqs. 1 and 2:

$$(1) \qquad P = \mathrm{PM} + M + \mathrm{Mi} + \mathrm{BA}$$

where P is net production, PM is mortalities due to predation, M is other mortalities, Mi is migration, and BA is biomass accumulation. The predation mortality term, PM, is used to link predator and prey species, and consumption, Q, is defined as

$$(2) \qquad Q = P + \mathrm{NA} + R$$

where NA is egested food and R is respiration. A detritus compartment was the recipient of flows originating from M and NA.

Ecotrophic efficiency (EE) is the fraction of production that is consumed by a higher trophic level or caught within the system (including net migration). EE for each compartment should be <1, as the underlying mass-balance condition implies that components of the system could only consume what has been produced during the time period considered. Thus, EE cannot exceed 100%. Since EE was not used as an input, it could be used as a rough check of input parameters and ratios.

The following input variables were used for all living groups: biomass (B), P/B, and P/Q. In addition, the amount exported from the system by migration, or emerged biomass (E), an estimate of the percentage of unassimilated food (%NA), and diet composition (DC) were required as inputs for each ecological group. The annual food intake of each consumer, coupled with an estimate of DC, determines the grazing quota at the lower level.

The concept of trophic levels has been adopted for constructing the trophic network. Two different types of trophic level were used. (*i*) The position of a functional group within the food web was determined by assigning a fractional trophic level to each compartment as suggested by Wiegert and Owen (1971), Odum and Heald (1975), and Levine (1980) based on the quantitative composition of its diet: a trophic level of 1 was assigned to primary producers and detritus. Trophic levels of consumers were calculated as 1 + the weighted average of the prey's trophic level. (*ii*) For comparing size of flows, these fractional trophic levels have been reversed, using an approach suggested by Ulanowicz (1995), into discrete trophic levels sensu Lindeman (1942). The concept of discrete trophic levels is well known and widespread. Thus, when a group obtains 60% of its food as a herbivore and 40% as a first-order carnivore, the relevant fractions of the flow through the group are attributed to the herbivore level and the first predator level.

For model calculations the software package Ecopath 3.0 was used (Christensen and Pauly 1992*a*, 1992*b*, 1993*b*), which is designed for the construction and parametrization of mass-balanced ecosystem models. The program includes routines for balancing flows in an ecosystem and for estimating indices for ecosystem characterization.

Data preparation and ecological grouping

Model inputs of B, P, P/B, the ratio of consumption to biomass (Q/B), P/Q, E, and %NA for compartments were estimated as described below. Missing values for P/Q, NA, and DC were taken from the literature. All parameters were entered as dry mass per square metre (g DW·m^{-2}), rates being expressed on an annual basis. Biomass values were rounded

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Table 1. Basic input values used for the food-web analysis of the macroinvertebrate community in the Steina mountain stream.

Compartment	Biomass (g DW·m^{-2})	*P/B*·year^{-1}	Export, *E* (g DW·m^{-2}·year^{-1})	*P/Q*	NA
Aufwuchs algae	4.66	32.20	—	—	—
Microorganisms	14.50	15.66	—	0.24	0.20
Planariidae	0.08	8.10	—	0.20	0.24
Oligo & Nema	0.18	10.00	—	0.10	0.65
Acari	0.06	5.00	—	0.20	0.20
Tipul & Crust	0.07	4.24	0.05	0.10	0.65
Ephemeroptera	0.80	6.54	0.10	0.08	0.50
Leuc, Nem, & Taen	0.20	4.66	0.02	0.13	0.60
Perlo, Chloro, Perli	0.13	5.50	0.00	0.20	0.20
Ancy, Limni, Brachy	0.45	3.27	0.04	0.12	0.50
Rhy, Oreo, Sial, Polyc	0.08	4.20	0.25	0.35	0.25
Hydrops & Simul	0.64	4.75	0.23	0.12	0.51
Psycho & Antocha	0.02	3.79	0.01	0.10	0.65
Limne, Odo, Seri	0.53	4.64	0.32	0.12	0.60
Lim p, Ibi, Cera	0.17	4.62	0.17	0.13	0.25
Chironomidae	0.19	10.00	0.41	0.13	0.50
Salmo & *Oncorhyn*	3.88	0.44	—	0.40	0.20
Cottus gobio	0.71	1.20	—	0.23	0.20
Detritus	181.50	—	—	—	—

Note: DW is dry mass; *P/Q* is the ratio of production to consumption; NA is the nonassimilated part of the food; *P/B* is the annual ratio of production to biomass.

to 0.01 g DW·m^{-2} and *P/B* ratios, *P/Q* ratios, and NA to 0.01.

In the stream, 161 animal taxa were identified (Meyer 1991, 1992, 1994). With the objective of reducing the number of compartments to an amount that could be handled with some ease and still represent the typical features of the system, the original number of species was aggregated into 19 compartments by applying a series of ecologically relevant criteria, such as (*i*) type of biomass production (producer, consumer), (*ii*) type of food (plant, meat, detritus, mixed), (*iii*) mode of feeding (e.g., suspension feeder, deposit feeder, predator), (*iv*) production and (or) consumption rate, and (*v*) standing-stock biomass. The resulting set of compartments consisted of 14 groups of benthic macroinvertebrates, two groups of fishes, and one group each of primary producers, microorganisms, and detritus.

Aufwuchs algae

Ruhrmann (1990) determined *B* and primary production of epilithic algae in a 3-year quantitative study. *B* was 4.66 g DW·m^{-2} and primary production 150.0 g DW·m^{-2}·year^{-1} (Table 1). Macrophytes were rare in the Steina, if present at all, therefore they were not considered in the model calculations.

Microorganisms

This compartment includes bacteria and fungi of the stream sediment. Fischer et al. (1996) reported total hyporheic bacterial biomass of 2.7 g C·m^{-2} and production of 97 g C·m^{-2}·year^{-1}, which correspond to biomass of 5.4 g DW·m^{-2} and production of 194 g DW·m^{-2}·year^{-1}, respectively. The resulting annual *P/B* ratio of 35.9 is of the same order as that mentioned by Meyer (1988). Biomass of fungi amounted to approximately 5% of benthic organic matter, and a *P/B* ratio of 3.65 was assumed (Gessner and Chauvet 1994; M.O. Gessner, Department of Limnology, EAWAG/ETH, CH-6047 Kastanienbaum, Switzerland, personal communication). For bacteria and fungi, a compartment biomass of 14.5 g DW·m^{-2}, production of 227.1 g DW·m^{-2}·year^{-1}, and a *P/B* ratio of 15.66 were yielded. According to Dr. Oliver Dilly (Ökologie-Zentrum, Universität Kiel, Schauenburgerstraße 112, D-24118 Kiel, Germany, personal communication), NA of 0.2 was assumed. For fungi, the *P/Q* ratio was set at 0.5 (Joergensen 1995; Prescott et al. 1999). For bacteria, Fischer et al. (1996) estimated a ratio of 0.44 for production to respiration (*P/R*), yielding a *P/Q* ratio of 0.24 for this compartment. Microorganisms here were exclusively allocated to the decomposers (Table 2).

Planariidae

This compartment includes three species of Planariidae, *Polycelis felina*, Planariidae (non det.), and *Dugesia lugubris*. *Polycelis felina* had a 98.6% share in the compartment biomass. A *P/Q* ratio of 0.2 was used and NA was fixed at 0.24 (compare Manokov and Sorokin 1972; Schönborn 1992). DC estimates followed indications in Reynoldson and Bellamy (1975), Schönborn (1987), and Seaby et al. (1996).

Oligo & Nema

This compartment includes eight taxonomic groups differentiated by Meyer (1992). The most important representatives in terms of *B* (Meyer 1992) are *Stylodrilus heringianus* (0.1 g DW·m^{-2}), the Enchytraeidae (0.04 g DW·m^{-2}), *Eiseniella tetraedra* (0.02 g DW·m^{-2}), and *Haplotaxis gordioides gordioides* (0.01 g DW·m^{-2}). For the other groups, $B <$ 0.002 g DW·m^{-2}. A *P/Q* ratio of 0.10 was applied, based on Schönborn (1987) for *Chaetogaster*, Schönborn (1998) for *Nais* sp., and McNeill and Lawton (1970) for *Limnodrilus*.

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Table 2. Diet composition (%) for the individual compartments used in the model calculation of the trophic web of the Steina stream.

Prey group		Predator group																
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	Aufwuchs algae	—	0.10	0.06	—	0.03	0.20	0.02	0.35	0.95	—	0.16	0.05	0.37	—	0.02	—	0.02
2	Microorganisms	—	0.06	0.45	0.30	0.10	0.05	0.05	0.03	0.01	0.05	0.05	0.10	0.01	—	0.06	—	—
3	Planariidae	—	0.01	—	—	—	—	—	—	—	—	—	—	—	—	—	0.03	0.05
4	Oligo & Nema	—	0.12	—	0.02	0.01	—	0.01	—	—	—	0.01	—	—	0.06	—	0.03	0.12
5	Acari	—	—	—	—	—	—	—	—	—	0.02	—	—	—	0.02	—	0.01	0.03
6	Tipul & Crust	—	0.04	—	—	—	—	—	0.02	—	—	—	—	—	—	—	—	0.01
7	Ephemeroptera	—	0.15	0.01	0.10	—	—	0.01	0.10	—	—	0.05	—	—	0.15	0.01	0.10	0.25
8	Leuc, Nem & Taen	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	0.10	0.12
9	Perlo, Chloro, Perli	—	—	—	—	—	—	—	0.01	—	—	—	—	—	0.05	—	0.03	0.06
10	Ancy, Limni, Brachy	—	0.02	—	—	—	—	—	—	—	—	—	—	—	0.05	—	0.15	0.10
11	Rhy, Oreo, Sial, Polyc	—	—	—	—	—	—	—	—	—	0.03	—	—	—	—	—	0.01	—
12	Hydrops & Simul	—	—	—	—	—	—	—	0.12	—	0.10	0.02	—	—	0.12	—	0.10	0.10
13	Psycho & Antocha	—	—	—	—	—	—	—	—	—	0.02	—	—	—	—	—	—	0.01
14	Limne, Odo, Seri	—	0.10	—	—	—	—	—	0.05	—	0.10	—	—	—	0.10	—	0.20	0.01
15	Lim p, Ibi, Cera	—	—	—	0.08	—	—	—	—	—	0.04	0.01	—	—	0.01	—	0.02	0.01
16	Chironomidae	—	0.05	—	0.15	0.01	—	0.01	0.02	—	0.02	—	—	—	0.02	0.01	0.05	0.10
17	Salmo & Oncorhyn	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	*Cottus gobio*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	Detritus	1.00	0.35	0.48	0.35	0.85	0.75	0.90	0.30	0.04	0.48	0.60	0.85	0.62	0.22	0.90	—	—
	Import	—	—	—	—	—	—	—	—	—	0.13	0.10	—	—	0.20	—	0.17	0.01
	Total	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Note: For full names of prey groups and the origin of values see the text.

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Based on Ivlev (1953) for *Tubifex tubifex* and Brinkhurst and Austin (1979), NA was fixed at 0.65 of the amount consumed. DC estimates were taken from Löhlein (1998).

Acari

This compartment comprises 41 mostly rheophilic species of water mites identified by Meyer (1994): *Sperchon* dominated with regard to biomass (36%), followed by *Torrenticola* (28%), *Lebertia* (18%), and Hygrobatidae (11%). A *P/Q* ratio of 0.2 was used as indicated by Christensen and Pauly (1992*b*), Engelmann (1966), and McNeill and Lawton (1970). NA was fixed at 0.2 (Manokov and Sorokin 1972; Schönborn 1992). DC estimates followed references listed in Böttger (1970) and Proctor and Pritchard (1989).

Tipul & Crust

This compartment incorporates benthic Crustacea and Tipulidae (Diptera), based on their similar *P/Q* and *Q/B* ratios and their similar DCs and modes of feeding. The most important species in terms of *B* were *Tipula* sp. with 0.06 g DW·m^{-2} (= 84.8% of compartment biomass) and *Gammarus fossarum* with 0.01 g DW·m^{-2}. For a third species, *Asellus aquaticus*, $B < 0.1$ g DW·m^{-2}. No information was available about the emergence of adult Tipulidae, so the export for the compartment was calculated by assuming that the ratio of E to larval secondary production was 18.3% (Poepperl 2000*a*). A mean *P/Q* ratio of 0.10 was used, based on McNeill and Lawton (1970) and Pieper (1978). NA was fixed at 0.65 after and Pieper (1978). DC estimates followed indications in Marcus et al. (1978) and Sutcliffe et al. (1981).

Ephemeroptera

This compartment consists of 15 taxa of Ephemeroptera (Meyer and Poepperl 2003). The most important species were *Baetis* spp. with 35.8%, *Epeorus sylvicola* with 10.9%, *Ephemerella* spp. with 8.7%, and *Habroleptoides confusa* with 7.6% of compartment biomass. Bötsch (1988) used pyramid and rectangular traps to investigate *E* for adults, and determined a mean value of 0.10 g DW·m^{-2}·year^{-1} (Table 1). The *P/Q* ratio was fixed at 0.08 (Fisher and Gray 1983; Benke and Jacobi 1994; Wotton 1994) and NA at 0.5 (Manokov and Sorokin 1972; Fisher and Gray 1983; Schönborn 1992). The diet consisted mainly of detritus and aufwuchs algae (Wallace et al. 1987; Benke and Jacobi 1994).

Leuc, Nem, & Taen

This compartment consists of the Plecoptera, which are specialized as shredders. *Leuctra* sp. had a share of 65.5%, *Amphinemura sulcicollis* 19.0%, *Protonemura* sp. 9.8%, *Nemoura* sp. 5.4%, and *Taeniopteryx hubaulti* 0.3% of compartment biomass (0.2 g DW·m^{-2}). *E* was reorganized from the data of Bötsch (1988) by using a mean individual dry mass of 0.72 mg. A *P/Q* ratio of 0.13 and NA of 0.6 were used, as indicated by Oertli and Dall (1993). DC estimates were obtained from Jones (1950).

Perlo, Chlom, Perli

This compartment sums up the predatory Plecoptera of the Steina. *B* was 0.13 g DW·m^{-2} and *P* was 0.73 g DW·m^{-2}·year^{-1}. *Perlodes microcephala* dominated with regard to biomass (55.9%), followed by *Isoperla* sp. (30.6%), *Perla marginata* (7.9%), and Hygrobatidae (5.7%). A *P/Q* ratio of 0.2 was used, as indicated by Christensen and Pauly (1992*b*) and McNeill and Lawton (1970). NA was fixed at 0.2 (Manokov and Sorokin 1972; Schönborn 1992). DC estimates followed indications in Lucy et al. (1990) and Malmqvist et al. (1991).

Ancy, Limni, Brachy

Based on similar *P/B* and *Q/B* ratios, DCs, and modes of feeding, this compartment incorporates grazing species from different taxonomic groups. *B* was 0.45 g DW·m^{-2}. The most important in terms of biomass was the family Elmidae (56.3%), represented by *Limnius perrisi* with 42.3%, *Esolus angustatus* with 6.8%, and *Elmis* sp. with 6.8%, followed by the gastropod *Ancylus fluviatilis* with 30.9% The remaining taxonomic groups in this compartment each had a share of less than 5.2% biomass. E was adopted from investigations by Bötsch (1988). The *P/Q* ratio was established at 0.12 (Jacobsen and Sand-Jensen 1994; Wotton 1994; Benke and Wallace 1997) and NA at 0.5 (Streit 1975; Jacobsen and Sand-Jensen 1994). DC estimates were obtained from Becker (1990) and Wallace et al. (1987).

Rhy, Oreo, Sial, Poly

This compartment includes different predatory representatives of Trichoptera, Megaloptera, Coeloptera, and Hydrozoa. The most important taxon was *Rhyacophila* sp., which had a 87% share of compartment biomass (0.08 g DW·m^{-2}). The remaining representatives, which contributed between 5.7% and 0.8% to compartment biomass, are, in order of decreasing biomass, *Oreodytes rivalis*, Hydrozoa, *Sialis fuliginosa*, *Polycentropus* sp., and *Plectrocnemia* sp. Export was investigated by Bötsch (1988). From indications in Manokov and Sorokin (1972), McNeill and Lawton (1970), and Schönborn (1992), a *P/Q* ratio of 0.35 and NA of 0.25 were calculated. The DC estimate for the compartment was obtained by summarizing indications for the different representatives (Malmqvist and Sjöström 1984; Wallace et al. 1987) though their individual DCs (Table 2), which often vary according to the availability of prey.

Hydrops & Simul

Five species of Hydropsychidae and three species of Simuliidae were identified by Meyer (1992). *Hydropsyche* sp. had a biomass of 0.57 g DW·m^{-2} (89.38%) and Simuliidae 0.07 g DW·m^{-2} (10.7%). *E* for Hydropsychidae was calculated from the data of Bötsch (1988) as mean value for both pyramid and rectangular traps. Semmler (1988) determined a number of 59 individuals of Simuliidae emerging from an area of 1 m^2·year^{-1}, and *E* was calculated by multiplying this value by an individual body mass of 1.2 mg (Poepperl 1987). The *P/Q* ratio was fixed at 0.12 (McNeill and Lawton 1970; Ladle et al. 1972; Poepperl 2000*b*) and NA at 0.51 (Ladle et al. 1972; Wotton 1994). DC was calculated after Wallace et al. (1987) and Benke and Wallace (1997).

Psycho & Antocha

This compartment consists of deposit-feeding Psychomyiidae and Diptera (except Chironomidae, which compose a separate compartment). Psychodidae contributed 58% to compartment biomass, Psychomyiidae 37%, *Antocha* sp. 4.8%, and Dixidae 0.2%. *E* was calculated by multiplying the number of emerged Psychodidae and *Antocha* sp.

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(Semmler 1988) by individual masses of 0.13 and 1.7 mg, respectively (from a mean of 7 and 5 taxa, respectively, listed in Poepperl 1987). A mean *P/Q* ratio of 0.10 was assumed, based on McNeill and Lawton (1970). NA was fixed at 0.65 after Schröder (1981). The species in this compartment feed mainly on detritus (Merritt and Cummins 1996).

Limne, Odo, Seri

This compartment comprises the species of Trichoptera that are shredders. Limnephilidae have a 64.3% share of biomass (0.53 g DW·m^{-2}), *Odontocerum albicorne* 21.1%, *Sericostoma* sp. 10.4%, and *Micrasema* sp. 4.2%. *B* values for adults were taken from the investigations of Bötsch (1988). The *P/Q* ratio was established at 0.12 (Iversen 1980; Jacobsen and Sand-Jensen 1994; Benke and Wallace 1997). NA was fixed at 0.6, the mean of values from different populations investigated by Otto (1974) and Jacobsen and Sand-Jensen (1994). Organisms in this compartment feed mainly on detritus and aufwuchs algae (Wallace et al. 1987).

Lim p, Ibi, Cera

This compartment consists of three species of predatory Limoniidae (Lim P) (Meyer and Poepperl 2003) combined with Athericidae, Ceratopogonidae, Empididae, and Tabanidae. The most important species were *Dicranota* sp. with 44.5%, *Hexatoma* sp. with 31.5%, *Pedicia* sp. with 10.6%, and *Ibisia marginata* with 8.6% of compartment biomass. Export (*E*) consisted mainly of emerged Empididae and was calculated by multiplying the abundance of emerged individuals (Semmler 1988) by a mean individual mass of 0.38 mg DW (Poepperl 1987). A *P/Q* ratio of 0.13 (Tilly 1968; McNeill and Lawton 1970) and NA of 0.25 were used (Manokov and Sorokin 1972; Schönborn 1992; Mathews 1993). Ceratopogonidae feed mainly on detritus and algae but ingest food of animal origin as well (Mayer 1934).

Chironomidae

B was determined by Meyer (1992) and *P* was estimated by Meyer and Poepperl (2003) using a *P/B* ratio from the literature. For the year 1987 Semmler (1988) calculated *E* of 0.95 g DW·m^{-2}·year^{-1}. In that year, larval production of Chironomidae was more than two times higher than in the years 1986 and 1988, therefore the biomass calculated by Semmler (1988) was multiplied by a factor of 0.43 to obtain the value used in the present model. A *P/Q* ratio of 0.13 was used, following Tilly (1968) and McNeill and Lawton (1970). NA was set at 0.5 after Mathews (1993). Wallace et al. (1987) provided indications of DC.

Salmo & Oncorhyn

Salmo trutta contributed 89% and *Oncorhynchus mykiss* 11% to the compartment biomass of 3.88 g DW·m^{-2}·year^{-1} (Table 1). The *P/B* ratio for 9 populations of brown trout reported in Waters (1977, 1992) varied between 0.5 and 5.0, and the lowest value, 0.2, was reported by Halfon and Schito (1993). Therefore, we did not take a value directly from the literature but used another approach: Meyer (1992) reported that for trout, consumption of benthic invertebrates was 3.58 g DW·m^{-2}·year^{-1}, and an additional 16.8% of total consumption (4.25 g DW·m^{-2}·year^{-1}) originated from terrestrial ecosystems. According to Winberg (1956), 20% of consumption was not assimilated. For the remaining 80%, it was assumed that *P* and *R* are equal (McNeill and Lawton 1970; Halfon and Schito 1993; Genoni et al. 2003). Based on these preconditions, the *P/B* ratio for the trout compartment was 0.44 and growth efficiency, i.e., *P/Q*, was 0.4. DC (by taxon, by dry mass) over a wide size range of fishes was investigated by Deller (1991) and Meyer (1992), based on stomach flushing following electrofishing runs.

Cottus gobio

B for *C. gobio* was determined by Meyer (1992). A *P/B* ratio of 1.2 was assumed according to Waters (1977). Meyer (1992) reported that consumption of zoobenthos was 3.7 g DW·m^{-2}·year^{-1}, and this amount is equal to 99% of consumption by *C. gobio*. Of the diet consumed by *C. gobio*, 1%, negligible in terms of mass, originates from terrestrial ecosystems (Table 2). A *P/Q* ratio of 0.23 results from the annual consumption and production of this compartment. For the other fish compartment, NA of 0.2 was used following Winberg (1956). DC (by dry mass) over a wide size range of individuals was investigated by Gädtgens (1989) and Meyer (1992), based on stomach flushing following electrofishing runs.

Detritus

The standing stock of leaves was approximately 130 g DW·m^{-2} (Gessner 1987). The detritus, which was deposited on the sediments and was of allochthonous as well as autochthonous origin, amounted to 51.5 g DW·m^{-2} (Pusch and Meyer 1989). Leaves imported in autumn contribute 61% (≈ 345 g·m^{-2}) of the annual import of coarse particulate organic matter, which amounts to 565 g DW·m^{-2}. The total annual import was 2200 g DW·m^{-2} of which, on the other hand, about 50% was exported (Gessner 1987), yielding a net import of 1100 g DW·m^{-2}·year^{-1} (J.L. Meyer et al. 1998).

DC estimates were assembled for ecological groups and species as described above. The input DC matrix for 17 compartments was prepared by calculating means weighted by consumption rates of constituent groups and species in each compartment (Table 2).

Results

The trophic web

The benthic primary producers and detritus in the stream maintain a large number of invertebrate primary consumers, which serve as food for predatory invertebrates and fishes (Fig. 1). As expected, the fish species were the top predators in the trophic web. *Cottus gobio* and the compartment "Salmo & Oncorhyn", consisting of *S. trutta* and *O. mykiss*, had the highest fractional trophic levels, 3.17 and 3.14, respectively (Table 3). A trophic level between 2.5 and 2.85 can be established for the four aggregated ecological groups Lim p, Ibi, Cera (predatory Diptera), Acari, Planariidae, and Rhy, Oreo, Sial, Polyc. Seven of the 19 compartments distinguished in the present model had trophic levels between 2.0 and 2.1: Psycho & Antocha, Leuc, Nem, & Taen, Chironomidae, Ephemeroptera, Ancy, Limni, Brachy, Limne, Odo, Seri, and microorganisms. They mainly fed on detritus and aufwuchs algae, which both had a trophic level of 1.0.

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Fig. 1. Trophic interactions and fluxes of dry matter within the trophic web of the Steina mountain stream. The area of each box is proportional to the logarithm of the biomass (in g dry mass (DW)·m^{-2}) of each group. *P* is production. Species are aggregated into individual ecological groups as described in the text. Ancyl: Ancy, Limni, Brachy; Aufw: Aufwuchs algae; Chiro: Chironomidae; Cottus: *Cottus gobio*; Ephem: Ephemeroptera; Hydrop: Hydrops & Simul; Leuctr: Leuc, Nem, & Taen; Limne: Limne, Odo, Seri; Limo: Lim p, Ibi, Cera; Microorg: Microorganisms; Oligo: Oligo & Nema; Perlo: Perlo, Chloro, Perli; Planar: Planariidae; Psycho: Psycho & Antocha; Rhya: Rhy, Oreo, Sial, Polyc; Salmo: Salmo & Oncorhyn; Tipu: Tipul & Crust. Flows >5 g DW·m^{-2}·year^{-1} are denoted by thick lines, and compartments with production >2 g DW·m^{-2}·year^{-1} have a thick border.

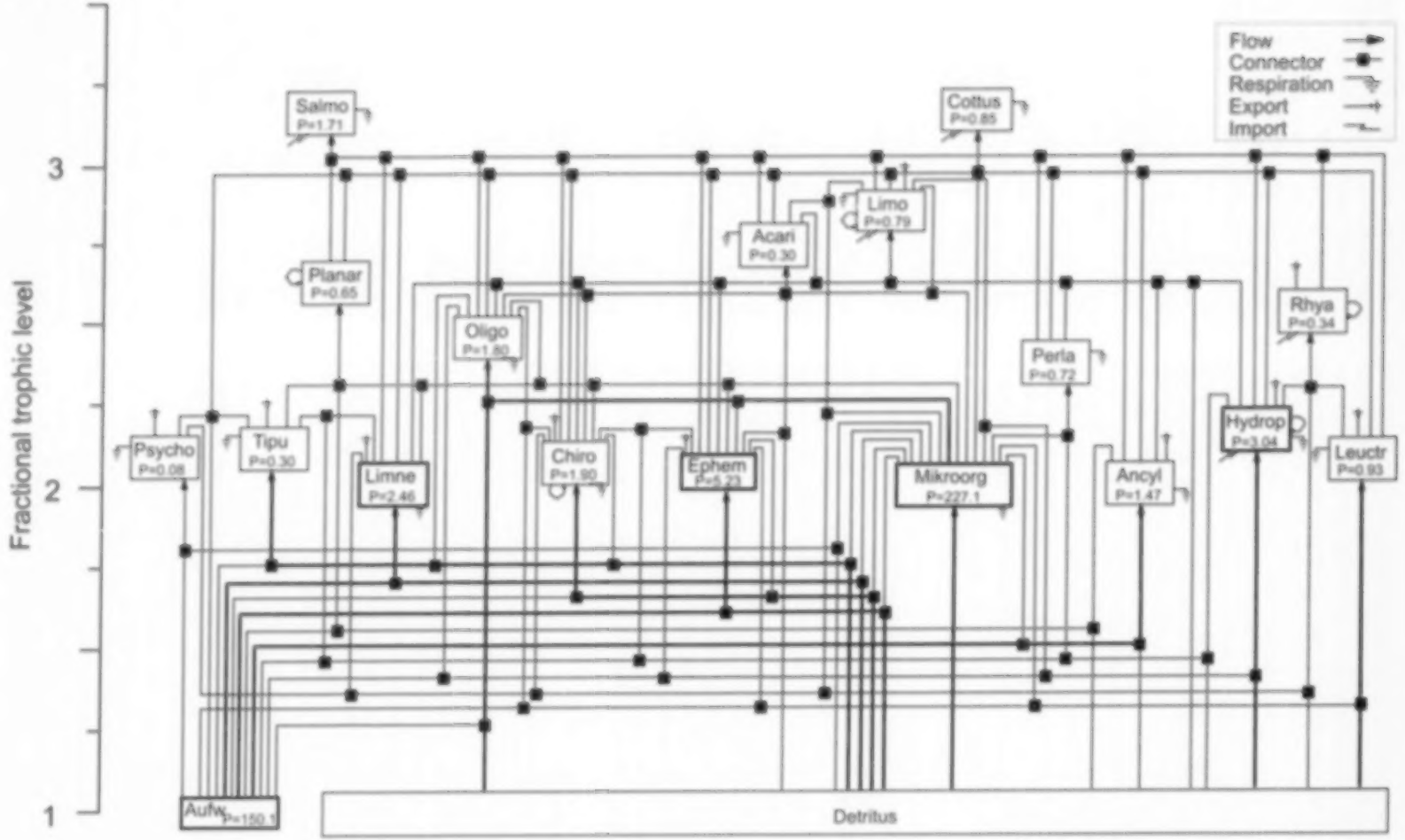

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Table 3. Selected output parameters of the food-web analysis.

Prey group	TL	*Q/B*	EE	P*EE	*R*	OI	*R/A*	*P/R*	D-flow
Aufwuchs algae	1.00	0.00	0.26	39.66	0.00	0.00	—	—	110.40
Microorganisms	2.00	65.25	0.07	15.37	529.83	0.00	0.70	0.43	400.92
Planariidae	2.63	40.50	0.53	0.35	1.81	0.34	0.74	0.36	1.08
Oligo & Nema	2.46	100.00	0.95	1.71	4.50	0.25	0.71	0.40	11.79
Acari	2.74	25.00	0.98	0.29	0.90	0.35	0.75	0.33	0.31
Tipul & Crust	2.13	42.40	0.97	0.29	0.74	0.12	0.71	0.40	1.94
Ephemeroptera	2.05	81.75	0.96	5.02	27.47	0.05	0.84	0.19	32.92
Leuc, Nem &Taen	2.09	35.85	0.97	0.90	1.94	0.09	0.68	0.48	4.33
Perlo, Chloro, Perli	2.38	27.50	0.96	0.69	2.15	0.28	0.75	0.33	0.74
Ancy, Limni, Brach	2.01	27.25	0.96	1.42	4.66	0.01	0.76	0.32	6.19
Rhy, Oreo, Sial	2.54	12.00	0.96	0.32	0.38	0.39	0.53	0.88	0.26
Hydrops & Simul	2.17	39.58	0.92	2.78	9.37	0.17	0.76	0.32	13.18
Psycho & Antocha	2.10	37.90	0.87	0.07	0.19	0.09	0.71	0.40	0.50
Limne, Odo, Seri	2.01	38.67	0.98	2.41	5.74	0.01	0.70	0.43	12.34
Lim p, Ibi, Cera	2.85	35.54	0.97	0.77	3.75	0.36	0.83	0.21	1.53
Chironomidae	2.08	76.92	0.97	1.84	5.41	0.08	0.74	0.35	7.37
Salmo & Oncorhyn	3.14	1.10	0.00	0.00	1.71	0.14	0.50	1.00	2.56
Cottus gobio	3.17	5.22	0.00	0.00	2.11	0.07	0.71	0.40	1.59
Detritus	1.00	—	0.62	—	—	0.57	—	—	—

Note: TL is the fractional trophic level; *Q/B* is the ratio of consumption to biomass; EE is ecotrophic efficiency; P*EE is predation mortality ($g\ DW \cdot m^{-2} \cdot year^{-1}$); *R* is respiration ($g\ DW \cdot m^{-2} \cdot year^{-1}$); OI is the omnivory index; *P* is production; *R/A* is the ratio of respiration to assimilation; *P/R* is the ratio of production to respiration; D-flow is the flow to detritus ($g\ DW \cdot m^{-2} \cdot year^{-1}$). For full names of prey groups see the text.

In the Steina the mean annual biomass was 3.6 $g\ DW \cdot m^{-2}$ for macroinvertebrates (Meyer 1991) and 4.59 $g\ DW \cdot m^{-2}$ for fishes. Apart from detritus, with a dry mass of 181.5 $g \cdot m^{-2}$ and import of 1100 $g \cdot m^{-2} \cdot year^{-1}$, compartments with biomass >1 $g\ DW \cdot m^{-2}$ were microorganisms, aufwuchs algae, and the group of *S. trutta* and *O. mykiss* (Table 1). The highest production values were observed for microorganisms (227.1 $g\ DW \cdot m^{-2} \cdot year^{-1}$) and aufwuchs algae (150.1 $g\ DW \cdot m^{-2} \cdot year^{-1}$). Secondary production of fish and macroinvertebrates amounted to 2.56 and 19.9 $g\ DW \cdot m^{-2} \cdot year^{-1}$, respectively (Meyer and Poepperl 2003). Invertebrate compartments with production >2 $g\ DW \cdot m^{-2} \cdot year^{-1}$ (Fig. 1) were Ephemeroptera, the deposit and suspension feeders Hydropsyche and Simuliidae, and the Trichoptera Limne, Odo, Seri, which live as shredders in the stream. The emergence of insects exported 1.6 $g\ DW \cdot m^{-2} \cdot year^{-1}$ from the system.

Apart from the trout compartment the *P/R* ratios ranged from 0.19 for Ephemeroptera to 0.88 for the predatory group Rhy, Oreo, Sial, Poly (Table 3). For the trout compartment, determination of the *P/B* ratio is based on the assumption that the *P/R* ratio was 1.0 (see the section "Data preparation and ecological grouping).

Transfer of matter between food-web compartments

Total consumption amounted to 1136.41 $g\ DW \cdot m^{-2} \cdot year^{-1}$, of which 1059.5 $g\ DW \cdot m^{-2} \cdot year^{-1}$ originated from detritus, 39.66 $g\ DW \cdot m^{-2} \cdot year^{-1}$ from autochthonous primary production, 15.37 $g\ DW \cdot m^{-2} \cdot year^{-1}$ from microorganisms, and 17.24 $g\ DW \cdot m^{-2} \cdot year^{-1}$ from invertebrates living in the stream. Hence, 93.2% of the dry mass consumed originated from detritus, 3.5% from aufwuchs algae, 1.4% from microorganisms, and 1.5% from invertebrates. With regard to the number of consumers, the most important food resources were detritus, microorganisms, aufwuchs algae, Ephemeroptera, and Chironomidae. Within the stream, *C. gobio*, *S. trutta*, and *O. mykiss* did not serve as a food resource for predators.

The main flows within the trophic network (>5 $g\ DW \cdot m^{-2} \cdot year^{-1}$) occurred between trophic levels 1 and 2, deriving from detritus and aufwuchs algae, as well as from microorganisms with a trophic level of 2.0 to the compartment consisting of oligochaetes and nematodes. Apart from the compartment Tipul & Crust, these main flows represent connections to the highly productive compartments with production >2 $g\ DW \cdot m^{-2} \cdot year^{-1}$ (Fig. 1). Inflows to the compartments of greatest quantitative importance were microorganisms (946.1 $g\ DW \cdot m^{-2} \cdot year^{-1}$) and Ephemeroptera (65.4 $g\ DW \cdot m^{-2} \cdot year^{-1}$) (Table 4). The model deals exclusively with the transfer of organic matter, therefore inflow to primary producers, such as the uptake of carbon dioxide, is not considered. Consumption of invertebrates and fishes was 182.3 and 8.0 $g\ DW \cdot m^{-2} \cdot year^{-1}$, respectively. Inflow to detritus was 610.0 $g\ DW \cdot m^{-2} \cdot year^{-1}$.

Predators consumed a large fraction of the 11 compartments that had a EE of >0.9 (Table 3). More than 90% of their production was consumed within the food web or exported from the system by insects emerging from the stream. A lower EE could only be observed in the compartments Psycho & Antocha, detritus, Planariidae, aufwuchs algae, and microorganisms. The EEs of these groups varied between 0.87 for Psycho & Antocha and 0.07 for microorganisms. Approximately 60% of material entering the detritus pool (EE = 0.62) was recycled to the living groups in the system. Almost 40% was accumulated and (or) exported out of the system. Primary producers contributed 18.1% (= 110.4 $g\ DW \cdot m^{-2} \cdot year^{-1}$) of the material flowing back to the detritus pool from the living groups in the system. Microorganisms contributed 65.7%, invertebrates 15.5%, and fishes 0.7%. Additionally, 1100 $g\ DW \cdot m^{-2}$ of terrestrial material

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Table 4. Flow matrix of the food-web analysis (all flows are given in g DW·m^{-2}·year^{-1}). Predation on a prey group is the sum of consumption values in the rows. Intake of a predator group is the sum of the values in a particular column.

		Predator group																	
Prey group		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
1	Aufwuchs algae	—	0.33	1.08	—	0.09	13.08	0.15	1.25	11.65	—	4.05	0.04	7.58	—	0.29	—	0.07	39.66
2	Microorganisms	—	0.19	8.10	0.45	0.30	3.27	0.36	0.10	0.12	0.05	1.27	0.08	0.20	—	0.88	—	—	15.37
3	Planariidae	—	0.03	—	—	—	—	—	—	—	—	—	—	—	—	—	0.13	0.18	0.34
4	Oligo & Nema	—	0.39	—	0.03	0.03	—	0.07	—	—	—	0.25	—	—	0.36	—	0.13	0.45	1.71
5	Acari	—	—	—	—	—	—	—	—	—	0.02	—	—	—	0.12	—	0.04	0.11	0.29
6	Tipul & Crust	—	0.13	—	—	—	—	—	0.07	—	—	—	—	—	—	—	—	0.04	0.24
7	Ephemeroptera	—	0.49	0.18	0.15	—	—	0.07	0.36	—	—	1.27	—	—	0.91	0.14	0.43	0.92	4.92
8	Leuc, Nem & Taen	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	0.43	0.44	0.88
9	Perlo, Chloro, Perli	—	—	—	—	—	—	—	0.04	—	—	—	—	—	0.30	—	0.13	0.22	0.69
10	Ancy, Limni, Brachy	—	0.07	—	—	—	—	—	—	—	—	—	—	—	0.30	—	0.64	0.37	1.38
11	Rhy, Oreo, Sial, Polyc	—	—	—	—	—	—	—	—	—	0.03	—	—	—	—	—	0.04	—	0.07
12	Hydrops & Simul	—	—	—	—	—	—	—	0.43	—	0.09	0.51	—	—	0.72	—	0.43	0.37	2.55
13	Psycho & Antocha	—	—	—	—	—	—	—	—	—	0.02	—	—	—	—	—	—	0.04	0.06
14	Limne, Odo, Seri	—	0.32	—	—	—	—	—	0.18	—	0.10	—	—	—	0.60	—	0.85	0.04	2.09
15	Lim p, Ibi, Cera	—	—	—	0.12	—	—	—	—	—	0.04	0.25	—	—	0.06	—	0.08	0.04	0.59
16	Chironomidae	—	0.16	—	0.23	0.03	—	0.07	0.07	—	0.02	—	—	—	0.12	0.15	0.21	0.37	1.43
17	Salmo & Oncorhyn	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00
18	*Cottus gobio*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00
19	Detritus	946.13	1.13	8.64	0.53	2.52	49.05	6.45	1.07	0.49	0.46	15.20	0.64	12.71	1.33	13.15	—	—	1059.5
	Import	—	—	—	—	—	—	—	—	—	0.13	2.53	—	—	1.21	—	0.73	0.04	4.64
	Total	946.13	3.24	18.00	1.51	2.97	65.40	7.17	3.57	12.26	0.97	25.33	0.76	20.49	6.03	14.61	4.27	3.70	1136.41

Note: For full names of prey groups see the text.

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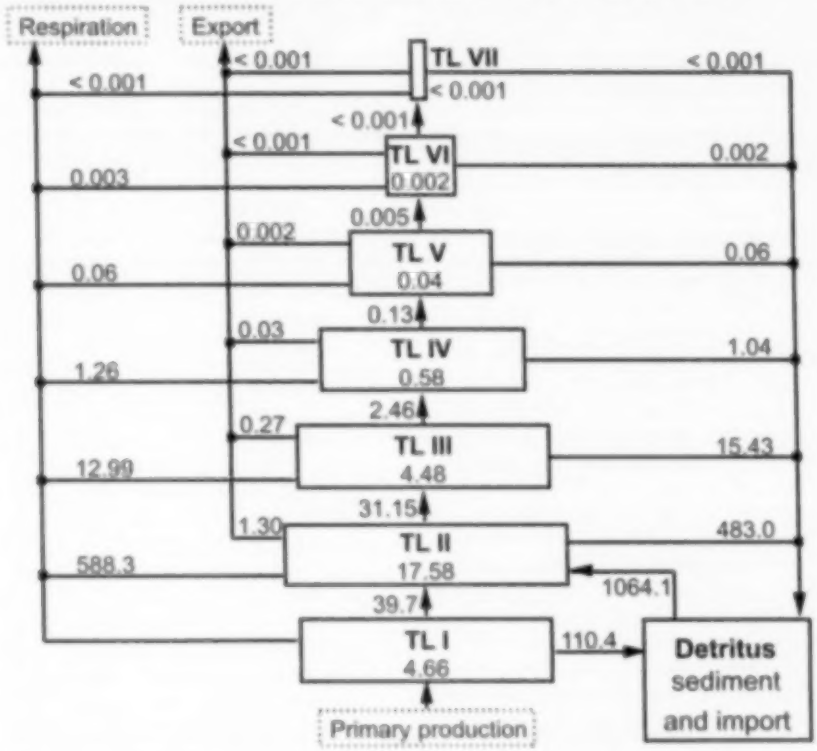
Fig. 2. Transfer of matter between discrete trophic levels (TL I to TL VII) separated into partial flows, consumption by the next trophic level, export from the system, respiration, and flow to detritus. All flows are given in g dry mass (DW)·m^{-2}·year^{-1} and biomass in g DW·m^{-2}. The area of each box is proportional to the logarithm of the biomass of each trophic level.



was imported annually and added to the detritus pool in the stream.

Transfer of matter between discrete trophic levels

To enable a comparison of size of flows with those reported in other studies, fractional trophic levels (presented in Table 3 and Fig. 1) have been converted using an approach suggested by Ulanowicz (1995) back into seven trophic levels sensu Lindeman (1942). Flows have been separated according to origin and destination (Fig. 2). As expected, biomass as well as the size of flows decreased continuously with increasing trophic level. The backflow to the detritus pool (610 g DW·m^{-2}·year^{-1}) from trophic levels I–VII corresponded to the amount described previously for the entire backflow from the individual compartments (Table 3).

Of the sum of all flows within the food web (2351 g DW·m^{-2}·year^{-1}), 93.2% (2192 g DW·m^{-2}·year^{-1}) was confined to trophic levels I and II; 593 g DW·m^{-2}·year^{-1} was being recycled directly to the detrital pool from trophic levels I and II.

Transfer efficiencies between successive discrete trophic levels were calculated as the ratio of the sum of exports plus the flow that is transferred from one trophic level to the next to the throughput on the concerned trophic level. Transfer efficiencies between discrete trophic levels could be determined by transforming these absolute values into relative values. The efficiencies of flows originating from primary producers, from detritus, and for combined flows are summarized in Table 5. Transfer efficiencies were generally low (<5%) except for level II for the transfer of material originating from primary producers (9.5%) and for level III for the transfer of detrital material originating from level I. For all flows combined, the lowest transfer efficiency was observed at discrete trophic level II and the highest at discrete trophic level III. At higher discrete trophic levels, efficiencies varied between 3.7% and 4.8%. To summarize the trophic situation of the stream, a large proportion of matter transfer at the lower discrete trophic levels was revealed.

Summary statistics and attributes of the food web

The sizes of system flows, such as consumption, export, respiratory flows, flows to detritus, system throughput, and production, are given by the selection of summary statistics listed (Table 6). Of the total system throughput of 2351 g DW·m^{-2}·year^{-1}, 48% was due to consumption (1136 g DW·m^{-2}·year^{-1}) and 26% to respiratory processes (603 g DW·m^{-2}·year^{-1}), and 26% originated in backflows to detritus (610 g DW·m^{-2}·year^{-1}). The sum of all production was about 400 g DW·m^{-2}·year^{-1}. The ratio of total primary production to total respiration was 0.25 and the ratio of total primary production to total biomass was 5.48. Matter is only passed up the trophic web to a moderate extent, a large amount of it being recycled to the detritus pool (Finn's cycling index = 25.2%). Total flow to detritus was several times larger than the system primary production. The overall system is to a large extent based on consumption

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Table 5. Biomass decrease (%) and transfer efficiencies (%) between discrete trophic levels.

	Discrete trophic level						
	I	II	III	IV	V	VI	VI
Biomass	—	37.2	25.5	13.0	7.5	4.5	*
Flows originating from producers	—	9.5	4.4	3.8	5.0	—	—
Flows originating from detritus	—	2.4	7.6	4.8	3.6	4.6	—
All flows	—	2.6	7.1	4.8	3.7	4.6	4.3

Note: Values refer to transfer from the previous trophic level. An asterisk indicates that no precise indication is available because of the low value.

Table 6. Selected summary statistics for the trophic web of the Steina mountain stream.

Sum of all consumption (g dry mass (DW)·m^{-2}·year^{-1})	1136.4
Sum of all exports (g DW·m^{-2}·year^{-1})	1.6
Sum of all respiratory flows (g DW·m^{-2}·year^{-1})	602.7
Sum of all flows into detritus (g DW·m^{-2}·year^{-1})	609.9
Sum of all flows into detritus, including import (g DW·m^{-2}·year^{-1})	1709.9
Total system throughput (g DW·m^{-2}·year^{-1})	2350.6
Total system throughput, including import (g DW·m^{-2}·year^{-1})	3450.6
Secondary production (g DW·m^{-2}·year^{-1})	249.6
Sum of all production (g DW·m^{-2}·year^{-1})	399.7
Calculated total net primary production (g DW·m^{-2}·year^{-1})	150.1
Total primary production / total respiration	0.25
Net system production (g DW·m^{-2}·year^{-1})	425.6
Total primary production / total biomass	5.48
Total biomass / total throughput	0.01
Total biomass, excluding detritus (g DW·m^{-2})	27.35
Connectivity index	0.34
Finn's cycling index (% of total throughput)	25.20
Omnivory index of the system	0.11

of detritus and imported organic material from terrestrial ecosystems.

Discussion

In the trophic network of the Steina stream, detritus and primary producers sustain a broad variety of benthic invertebrate consumers. These in turn serve as food for the upper levels, including fish and highly predatory invertebrates. Sculpin and the two trout species occupied trophic levels around 3.15, followed by predatory invertebrates with values up to 2.9. Mathews (1993) obtained similar results for the River Thames, reporting maximal fractional trophic levels of nearly 3 and similar values for predatory fish and invertebrates. As in other aquatic systems the majority of compartments have trophic levels ranging from 2.5 to 2.0, along with increasing importance of detritus and primary producers in their diet (i.e., Christensen and Pauly 1993*b*; Poepperl 2003; R. Poepperl and S. Opitz, unpublished data).

Macroinvertebrate biomass in the Steina amounted to 3.6 g DW·m^{-2} (Meyer 1991, 1992), which is well within in the range found in other mountain streams listed in Poepperl (1999) and Meyer and Poepperl (2003). Higher values are known mainly from unshaded lowland streams, but also from rivers as well as from lake outlets (Benke 1993). Secondary production of macroinvertebrates considerably exceeds that in other streams (Meyer and Poepperl 2003). The high value for the Steina becomes obvious from a listing of macroinvertebrate biomass and secondary production in 36 streams (Poepperl 1999). High secondary production of pollution-tolerant species is found in streams, which are organically enriched, and furthermore, production is generally higher in unshaded than in shaded reaches of streams as well as at the outlets of lakes (Poepperl 1999). The turnover ratio of 5.5 for invertebrates in the Steina matches well the ranges given in the literature (e.g., Benke 1993; Meyer and Poepperl 2003).

The *P*/*R* ratio could be used as a qualitative indicator of input. For the trout compartment, determination of the *P*/*B* ratio was based on the assumption that production and respiration had the same extent (Genoni et al. 2003) and therefore this *P*/*R* ratio could not be used as indicator. The remaining values ranged between 0.19 for Ephemeroptera and 0.88 for the predatory group Rhy, Oreo, Sial, Poly. All *P*/*R* values calculated by the model were in the range of values listed by McNeill and Lawton (1970) for 53 taxa.

The omnivory index is calculated as the variance of the trophic level of a consumer's prey group. The omnivory index can increase with the trophic level of a predator group because more prey groups become available to potential predators (Christensen and Pauly 1993*b*). This effect is reduced as the trophic level increases further and approaches the top predators, which feed on only a few groups.

Main flows could be identified between trophic levels I and II (Christensen and Pauly 1993*a*; Palomares et al. 1993) and are connected with highly productive compartments. As

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expected, consumption of several compartments was very low in the Steina compared with highly productive freshwater systems (Christensen and Pauly 1993*b*), therefore this stream — or perhaps mountain streams generally — can be classified as a low-productivity system (Benke et al. 2001). However, this assumption needs to be confirmed by means of further studies.

The system exerted high predation pressure (EE > 90%) on more than 60% of the compartments. The EEs of the compartments are in the same range as those of other studies, with maxima of nearly 95% (Mathews 1993; Palomares et al. 1993; R. Poepperl and S. Opitz, unpublished data). Generally, lower EEs were determined for all compartments by Poepperl (2003) for a lowland stream in northern Germany, but fish were not considered in the model because of missing data. Approximately 60% of material entering the detritus pool of the Steina (EE = 62%) is recycled to the living groups of the system. This EE value for sediment detritus is lower than the value for the River Thames (EE = 79%) calculated by Mathews (1993) and Berrie (1972). Seventy-four percent of primary production in the Steina flows back to the detritus pool and this is similar to the 83% reported for a lowland stream in northern Germany (Poepperl 2003), 60% for the River Thames (Mathews 1993), and 85% for the River Garonne (Palomares et al. 1993). This value justifies to some extent the model routine of assigning a uniform value of 1 to detrital matter, irrespective of its origin, and a uniform value of 2 to microorganisms.

Many input data used for the model calculations were investigated directly for the Steina. Biomass and production of invertebrates, periphyton biomass and primary production, input and processing of particulate organic matter, hyporheic respiration, biomass of and consumption fish species could be derived from various field and laboratory experiments. Some information, such as diet composition of some groups, and *P*/*Q* ratios, have been estimated using information from other systems. Using the same modelling approach Poepperl (2003) analyzed the sensitivity of the model and described that the mass-balanced model was relatively insensitive to parameter values for most groups. According to Christensen (1995) this is due to the wide variety of food items.

To compare sizes of flows, fractional trophic levels have been converted into discrete trophic levels sensu Lindeman (1942) using an approach suggested by Ulanowicz (1995). Seven discrete trophic levels can be distinguished. Flows have been separated according to origin or destination. As expected, biomass decreases continuously with increasing trophic level. The same effect can be observed for the quantity of flows. The backflow to detritus of 610 g DW·m^{-2}·year^{-1} from trophic levels I to VII corresponds to the amount given previously for the entire backflow from single compartments.

Of total system throughput (2351 g DW·m^{-2}·year^{-1}), 93.2% is confined to trophic levels I and II. This value is comparable to the 98.8% for a north German lowland stream (Poepperl 2003) and the 90% for the littoral zone of a north German lake (R. Poepperl and S. Opitz, unpublished data). Our value for the Steina agrees with values from other systems (Christensen and Pauly 1993*b*).

Transformation of absolute values of flows into relative ones gives an indication of transfer efficiencies between discrete trophic levels. Transfer efficiencies of flows originating from both primary producers and detritus varied between 2.6 and 7.1. Values for primary producers reflect the direct flow to detritus with a low efficiency for producers from discrete trophic levels I to II followed by low efficiencies also at higher trophic levels. Since Lindeman (1942) it has often been assumed that trophic transfer efficiencies in ecosystems vary around 10%, so that one-tenth of matter or energy entering a trophic level is transferred to the next trophic level (this value is only approached by the transfer between trophic levels I and II for flows originating from producers) and that trophic transfer efficiencies gradually decrease at higher trophic levels (Christensen and Pauly 1993*a*; Hairston and Hairston 1993). The transfer efficiencies between 7.1 and 2.6 presented here are generally low but are of the same order of magnitude as those reported for the River Garonne (0.2–10.1; Palomares et al. 1993), the River Thames (0.0–8.3; Mathews 1993), a north German lowland stream (0.2–6.0; Poepperl 2003), and the mesohaline Chesapeake Bay (average of 9.6; Baird and Ulanowicz 1989). Christensen and Pauly (1993*a*) compared the trophic transfer efficiencies of a number of (mainly marine) ecosystem models and concluded that the efficiencies vary, because of both system- and model-specific characteristics. Hairston and Hairston (1993) posit that the structure of pelagic food webs leads to increased trophic efficiency and hence longer food chains than in than terrestrial food webs. In the Steina, efficiencies are low and the food chain is long compared with the results of Cohen (1994), who studied aquatic and terrestrial food webs (Irmler and Poepperl 1998). As described for the investigated stream, trophic efficiencies generally tend to be higher at lower trophic levels than at higher levels. A summary of the trophic situation in the Steina reveals that a large proportion of matter transfer occurs at the lower trophic levels. Very little matter is passed up the food web. A large amount is recycled to the detritus pool directly from the first and second trophic levels.

The selection of summary statistics shows the size of system flows such as consumption, exports, respiratory flows, flows into detritus, system throughput, and production. Additionally, the model provides information that can be used for an assessment of the developmental stage of an ecosystem and for an interecosystem comparison (Odum 1969; Christensen and Pauly 1992*a*).

System biomass, production, and consumption in the Steina are low compared with the River Thames (Mathews 1993), the Garonne River (Palomares et al. 1993), and a lowland stream (Poepperl 2003). There is a large transfer of matter at the lower levels. Total flow to detritus is larger than system net primary production. The community is thus driven by the flows passing through the detritus pool. Mathews (1993) reported a corresponding result for the River Thames (Berrie 1972). The overall system is based to a large extent on consumption of detritus and imported organic material from terrestrial ecosystems.

According to Finn's cycling index more than 25% of throughput is recycled within the system. Only 15% of 41 trophic webs assembled by Christensen and Pauly (1993*a*) show a higher cycling index than the food web of the Steina. Interpretation of the significance of the cycling index in relation to system maturity is still contradictory.

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Odum (1971) described how the ratio of total primary production to total system respiration (P_p/R) would develop as systems become more mature. In immature systems, primary production would grossly exceed total respiration (Christensen and Pauly 1993*a*). Lewis (1981), as well as Christensen and Pauly (1993*a*), found P_p/R ratios for 25 and 41 ecosystems, respectively, the majority ranging from 0.8 to 3.2. The P_p/R ratio for the community in the Steina was only 0.25. Values lower than 0.8 were found by Christensen and Pauly (1993*a*) only for five ecosystems, but they also reported that in the majority of systems, omission of microorganism activity led to an underestimation of respiration. We conclude that in systems from which microorganism activity is excluded, it can be expected that the P_p/R ratio will be overestimated. In the River Thames, primary production (mainly phytoplankton) had a 67% share of total system production and the P_p/R ratio was 1.3 (calculated after data from Mathews 1993), whereas in the Steina, autochthonous primary production has only a 37% share and the P_p/R ratio is only 0.25. The P_p/R ratio for the Steina is close to the lower limit of the range reported by Christensen and Pauly (1993*a*), and according to the above concept of Odum (1969) the stream would be classified as a subsidized system. But for streams like the Steina this concept should be regarded with caution because stream processes are tied to those in the whole landscape. So succession in a stream can occur very quickly relative to succession in the forest around it (Valett et al. 2002). A stream in a mature forest ought to have lower P/R ratio than a stream in a clearcut, but this is because the forest, not the stream, controls this process.

Other parameters and ratios such as total B, total P, total C, P/B ratio, ratio of total biomass to system throughput, connectivity index, and system omnivory index yield contradictory estimates of developmental stage and maturity of the trophic web. This is due to a lack of comparative studies, but could as well be the consequence of blank spots in the field of theoretical systems' ecology. A more detailed discussion of this subject will follow in the future, focusing on indicators for characterizing the ecological integrity of freshwater ecosystems. In conclusion, the Steina ecosystem is among the first comprehensive mass-balanced networks presented for Central European streams, completing the recently performed energetic and biogeochemical analyses of this system (Genoni et al. 2003). In conclusion, some important aspects should be mentioned: food-web analyses tend to be predominantly hierarchical, and it is also argued that "horizontal" processes — such as competition — influence food-web structure and dynamics. In our study we have also neglected the fact that ecological networks are dynamic and work at various spatial and temporal scales, not only in terms of biotic interactions, but also, for instance, environmental variables (Gaedke 1995; Pahl-Wostl 1995). Hershey and Peterson (1996) point out that specific constraints such as environmental factors like the geographic distribution of species, geomorphology, substratum characteristics, gradient, riparian characteristics, and temperature, and interspecific interactions, influence food-web structure and dynamics.

A further interesting aspect to consider is whether, instead of using published consumption estimates for the different species, assigning percentages of invertebrate taxa to a mixture of specific food categories (based on a 10-point classification system; Moog 1995; Schmedtje and Colling 1996) would yield the same or quite different results from our data set. Finally, a calculation of the summarized food web for the Steina, which will be performed in the near future, is expected to vary among seasons and hence will take into account the environmental setting of the system.

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Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*)

Jonathan W. Moore and Daniel E. Schindler

Abstract: Anadromous and semelparous salmon transport nutrients from the ocean to fresh waters when they return to spawn and die, a process inspiring a large body of research on the role of salmon-derived nutrients in coastal ecosystems. However, salmon also transport nutrients out of fresh waters when they migrate to the ocean as smolts. Using a total of 76 years of age-specific smolt-migration and adult-escapement data, we calculated the amounts of nitrogen and phosphorus that sockeye salmon (*Oncorhynchus nerka*) imported and exported from four major systems in Bristol Bay, Alaska. Smolts removed an average of 16% of the phosphorus and 12% of the nitrogen that their parents transported into fresh waters. The percentage of parental nutrients that smolts exported varied through time and among sites, ranging from 1% to 65% of the phosphorus and from less than 1% to 47% of the nitrogen. In systems where smolts were larger, they exported a higher percentage of nutrients. Depending on the strength of density-dependence, smolts could theoretically export more nutrients than their parents import to freshwater ecosystems at low spawning densities. Ignoring nutrient export by outgoing smolts will consistently lead to overestimation of nutrient import by Pacific salmon to freshwater ecosystems.

Résumé : Les saumons anadromes et sémelpares transportent des nutriments de l'océan vers les eaux douces lorsqu'ils retournent pour frayer et mourir; c'est un phénomène qui a suscité un nombre important de recherches sur le rôle des nutriments provenant des saumons dans les écosystèmes côtiers. Cependant, les saumons exportent aussi des nutriments lorsque les saumoneaux émigrent vers l'océan. Des données réparties sur 76 années sur la migration des saumoneaux en fonction de l'âge et sur l'échappement des adultes nous ont servi à calculer les quantités d'azote et de phosphore que les saumons rouges (*Oncorhynchus nerka*) importent et exportent dans quatre systèmes hydrographiques majeurs dans la baie de Bristol, Alaska. Les saumoneaux retirent en moyenne 16 % du phosphore et 12 % de l'azote que leurs parents ont apportés dans les eaux douces. Les pourcentages des nutriments parentaux que les saumoneaux exportent varient dans le temps et d'un site à un autre, allant de 1 % à 65 % du phosphore et de moins de 1 % à 47 % de l'azote. Les saumoneaux exportent un pourcentage plus grand de nutriments dans les systèmes qui ont des saumoneaux de plus grande taille. Selon l'intensité de la dépendance de la densité, les saumoneaux pourraient en théorie exporter plus de nutriments que leurs parents en importent dans les écosystèmes d'eau douce lorsque les densités de reproducteurs sont faibles. Si l'on néglige de considérer l'exportation par les saumoneaux qui émigrent, on surestime systématiquement l'importation de nutriments vers les eaux douces par les saumons du Pacifique.

[Traduit par la Rédaction]

Introduction

Migrating adult anadromous and semelparous salmon transport massive quantities of nutrients from oceans to the fresh waters where they spawn and die (Larkin and Slaney 1997; Schmidt et al. 1998; Gresh et al. 2000). For example, adult Pacific salmon historically contributed over 3 million kg of nitrogen and 0.36 million kg of phosphorus each year to the Columbia River ecosystem (Gresh et al. 2000). This ecosystem resource subsidy (Polis et al. 1997) directly and indirectly fuels numerous species of flora and fauna of coastal ecosystems (Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). Declines in salmon populations have raised concerns about how reductions of this subsidy will impact specific species as well as the overall productivity and biodiversity of coastal ecosystems (Willson and Halupka 1995; Naiman et al. 2002; Schindler et al. 2003).

However, salmon do not transport nutrients unidirectionally from oceans to fresh waters as adults returning to spawn. The migration of salmon smolts from fresh waters to the ocean represents a flow of nutrients from fresh waters to the ocean. The term smolt refers to juvenile salmon that have undergone the physiological and behavioral changes that occur prior to migration to marine or estuarine ecosystems (Groot and Margolis 1991). Juveniles of some species and populations of salmon migrate out of fresh waters immediately after emerging (especially *Oncorhynchus gorbuscha* and *Oncorhynchus*

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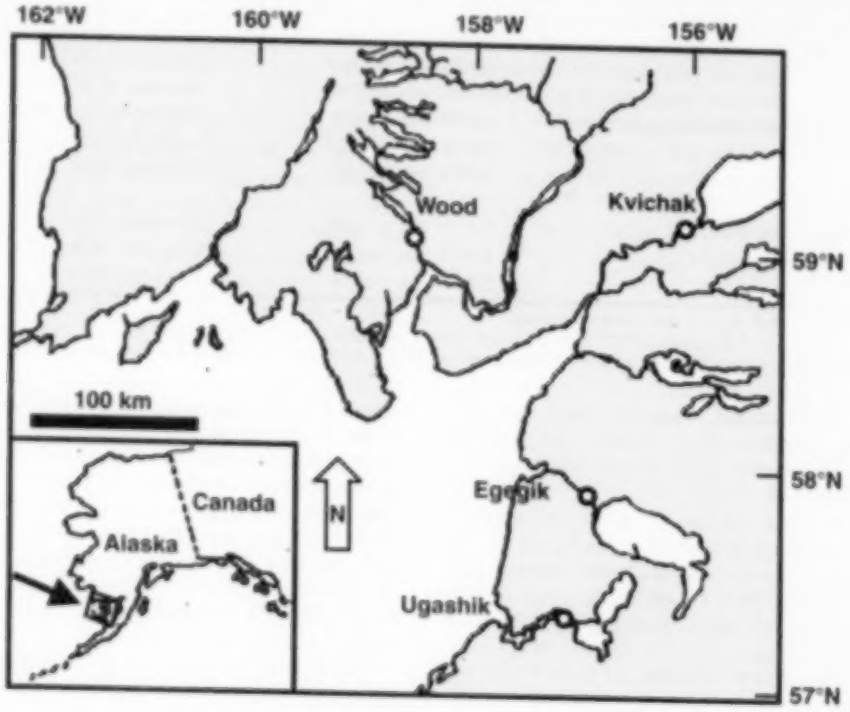
Fig. 1. Map of Bristol Bay, Alaska, USA, showing the four systems where data used in our analyses were obtained for analyzing nutrient transport by sockeye salmon (*Oncorhynchus nerka*) (modified from Hilborn et al. 2003). The locations of smolt sampling sites are indicated by circles.



keta), while other species and populations spend up to several years in fresh waters prior to migration (Groot and Margolis 1991).

This aspect of nutrient transport by anadromous salmon is usually ignored (e.g., Larkin and Slaney 1997; Gresh et al. 2000), or dismissed by citing that from 95% to over 99% of the mass of anadromous salmon is acquired in the ocean, implying that smolt nutrient export from fresh waters is inconsequential. However, this assumes that the number of smolts leaving fresh waters is equal to the number of adults returning to fresh waters, even though ocean mortality of smolts is often substantial (e.g., >80%; Burgner 1991). To the best of our knowledge, no study has systematically analyzed the export of nutrients from freshwater systems by smolts across systems and years. However, in previous studies of a specific system it has been estimated that smolts export from 6.7% to 24.2% of the nutrients that their parents imported (Donaldson 1967; Naiman et al. 2002). Thus, how much of the nutrients imported to fresh waters by returning adults is exported by out-migrating smolts remains unknown. In other words, while previous studies have quantified the nutrients that adult salmon transport to fresh waters (Larkin and Slaney 1997; Schmidt et al. 1998; Gresh et al. 2000), we do not know how salmon impact net nutrient transport. For these reasons we quantified the relative magnitudes of nutrient transport by out-migrating smolts and returning adult sockeye salmon (*Oncorhynchus nerka*).

Using historical smolt and adult escapement data from four major sockeye salmon nursery systems in Alaska, we calculated the amounts of nitrogen and phosphorus that anadromous sockeye salmon import to and export from fresh waters, using a total of 76 years of data from four different systems. Based on these calculations, we found that sockeye salmon are consistent net importers of nutrients to fresh waters, but that out-migrating smolts often export a substantial fraction of the nutrients that their parents imported, and that the percentage exported varies considerably across space and time.

Materials and methods

We analyzed smolt and escapement data from four systems (Fig. 1) that comprise a large percentage of the sockeye fishery of Bristol Bay, Alaska (Hilborn et al. 2003). The Egegik system consists of the King Salmon River and the Egegik River and all of their tributaries. The Kvichak system consists of the Kvichak River, which drains Iliamna Lake and Lake Clark. The Wood River system consists of the Wood River, draining all of the Wood River lakes. The Ugashik system is located on the Alaska Peninsula and is dominated by flows from the Upper and Lower Ugashik lakes. These systems are located around 158°W and 58°N. The vegetation of these watersheds is a mix of spruce, alder, and tundra. Sockeye salmon is the most common species of Pacific salmon in these systems, although other species do spawn in these watersheds. Over the last 40 years, the total annual run to these systems has averaged 24 million sockeye. Over this period a total of 0.8 billion kg of sockeye

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Table 1. Description and source of constants considered for calculations.

Description	Value used	Source
Spawners		
Phosphorus content ($C_{P,adult}$)	0.36% wet weight	Larkin and Slaney 1997
	0.38% wet weight*	Donaldson 1967
	0.48% wet weight	Mathisen et al. 1998
Nitrogen content ($C_{N,adult}$)	2.67% wet weight	Mathisen et al. 1998
	3.04% wet weight*	Larkin and Slaney 1997
	3.30% wet weight	Ramseyer 2002
Smolts		
Phosphorus content ($C_{P,smolt}$)	0.43% wet weight*	Donaldson 1967
Nitrogen content ($C_{N,smolt}$)	2.49% wet weight*	Kline and Willette 2002
	2.49% wet weight	Ramseyer 2002†

*Value was used in the analyses presented.
†Values from Ramseyer (2002) were calculated from a regression ($r^2 > 0.99$) of sockeye salmon (*Oncorhynchus nerka*) body mass and nitrogen content for the average-sized smolt or spawning sockeye.

have spawned in these systems, while the fishery has harvested an additional 1.6 billion kg of sockeye. The dynamics of the last century of fisheries in the Bristol Bay are further described by Hilborn et al. (2003).

We reconstructed gross nutrient transport using smolt-migration and adult-escapement data from the Egegik, Wood, Kvichak, and Ugashik systems and published nutrient contents of sockeye. We analyzed a total of 76 years of data where age- and size-specific data on escapement of adult sockeye overlapped with age- and size-specific smolt data: 17 years from Egegik, 29 from Kvichak, 13 from Wood, and 17 from Ugashik.

Data used in these analyses were collected by the Alaska Department of Fish and Game (Hilborn et al. 2003; Weiland et al. 2003). Escapement data were collected via visual counting towers located on the major rivers that lead into these lake systems. Thus, these counting towers provide estimates of escapements of sockeye after they have passed the fisheries at the mouths of these systems (Weiland et al. 2003). Age composition and weight-at-age of the escapement for each system in each year were calculated by sampling scales and masses of large numbers of returning adults to determine the percent composition of the different age classes in relation to the overall salmon return.

Data on out-migrating smolts were collected with the aid of fyke nets and hydroacoustic equipment near the mouths of the rivers flowing out of each system, prior to smolts entering the estuarine habitats (Crawford 2001). The size and age composition of the out-migrating smolt population was estimated using samples collected from fyke nets. Smolt mass and freshwater age based on scale annuli were taken from a large sample (around 400 individuals) of smolts every day during migration, which typically lasts 3 weeks (Crawford 2001). Thus, these data not only give the number of out-migrating smolts from each system, but also the age composition of the population and the average mass of each age class for each year.

For each brood year, t, we calculated the gross import of a nutrient, n, as

$$\text{Import}_{n,t} = \sum_{age} (E_{age,t} \cdot \text{AM}_{age,t} \cdot C_{n,\text{adult}})$$

where $E_{age,t}$ is the age-specific escapement (in numbers of returning adults) in year t, $\text{AM}_{age,t}$ is the average mass of that age class of spawners in year t, $C_{n,\text{adult}}$ is the percent wet weight content of the nutrient of interest (phosphorus or nitrogen) in spawning sockeye bodies summed across all age classes in the escapement in year t. Because sockeye achieve >99% of their lifetime growth in the marine ecosystem and because of tissue turnover (Burgner 1991), we are assuming that nutrients from returning adult sockeye are completely of marine origin.

We calculated the gross export of nutrients by smolts produced from brood year t of spawners as

$$\text{Export}_{n,t} = \sum_{age} (S_{age,t} \cdot \text{SM}_{age,t} \cdot C_{n,\text{smolt}})$$

Thus, for a given brood year t, gross nutrient export by smolts equals the number of outgoing smolts of a given age class ($S_{age,t}$) times the average mass of those smolts (SM_t) times their nutrient content by weight ($C_{n,\text{smolt}}$). We calculated import and export on a brood-year basis; in other words, these smolts did not all leave in the same year, but they were sired by the same population of spawners. We are assuming that out-migrating smolts are completely of freshwater origin, and this is supported by the observation that juvenile salmon quickly lose the isotopic signature of their parents (Kline et al. 1993).

We used previously published values or relationships for the phosphorus and nitrogen nutrient content of sockeye carcasses and smolts (Table 1). Although previous estimations of nutrient concentrations are relatively consistent, there are slight differences due to either measurement error or variability among sockeye populations (Table 1). Therefore, for constants where there were multiple estimates, we used the intermediate estimate for our calculation.

To explore the possible effect of density-dependent juvenile growth and survival on the balance between nutrient import and export by sockeye, we fit Beverton–Holt stock–recruit relationships to nutrient fluxes calculated above for each system (Beverton and Holt 1993). The Beverton–Holt function is often used to characterize density-dependence in salmon populations (e.g., Liermann and Hilborn 1997). Salmon populations often exhibit density-dependence; for example, higher numbers of spawning salmon often produce

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smolts that are characterized by a lower freshwater survival rate (Koenings and Burkett 1987) or smaller size (Eggers and Rogers 1987). In nutrient currency, the Beverton–Holt stock–recruit function is expressed as

$$\text{Export} = \frac{a \cdot \text{import}}{b + \text{import}}$$

where the export of nutrients in brood year t is a function of the import of nutrients for that brood year. We fit the unknown parameters a and b to observed data by minimizing the negative log-likelihood of the model (Hilborn and Mangel 1997) using brood-year-specific export and import (in kilograms of phosphorus) and assuming log-normally distributed errors. We focused on phosphorus because it is a limiting nutrient for these fresh waters (Goldman 1960; D.E. Schindler, unpublished data). However, because the nitrogen to phosphorus (N:P) ratio of smolt was 73% of the N:P ratio of adult salmon, the percentage of adult nitrogen that smolt export was 73% of the percentage of phosphorus exported. We also used hypothetical stock–recruit relationships of systems with intermediate (a = 10 000, b = 30 000) and strong (a = 10 000, b = 3000) density-dependence to illustrate that nutrient export by smolts could theoretically be larger than import by adults at low spawner densities. These values for the Beverton–Holt relationship are arbitrary, and are chosen to illustrate the potential impacts of density-dependence on the percentage of parental nutrients that smolt export. Based on the predicted relationship between import and export, we calculated the predicted percentage of parental nutrients that smolts export across a gradient of escapements (import).

Results

Anadromous sockeye transported large quantities of nitrogen and phosphorus both as adults and as smolts. However, sockeye consistently acted as net importers of nutrients (Fig. 2). Averaged across systems and years, smolt exported 16% of the phosphorus and 12% of the nitrogen that their parents imported. Because the N:P ratio of adult sockeye (7.92) was higher than that of smolts (5.76), smolt consistently exported a smaller fraction (73%) of parental nitrogen than phosphorus.

In the Egegik system, adult salmon transported 13 500 ± 4600 kg (mean ± 1 standard deviation) of phosphorus and 106 000 ± 36 000 kg of nitrogen into freshwater nursery ecosystems each year. Smolts transported 23.3 ± 13.9% of phosphorus and 17.0 ± 10.1% of nitrogen back to the ocean, corresponding to 2900 ± 1500 and 16 530 ± 8943 kg of phosphorus and nitrogen, respectively, each year.

The Kvichak system was characterized by higher levels of nutrient transport that were highly variable through time: adult salmon transported 50 200 ± 40 800 kg of phosphorus and 397 000 ± 324 000 kg of nitrogen each year. Smolts transported 5000 ± 3800 kg of phosphorus and 29 054 ± 21 961 kg of nitrogen, which translates to 11.8 ± 8.4% of the phosphorus and 8.6 ± 7.0% of the nitrogen that their parents transported from the ocean.

The Wood River system had more consistent nutrient transport by sockeye: adults transported 12 700 ± 5600 kg of phosphorus and 101 000 ± 44 400 kg of nitrogen each year.

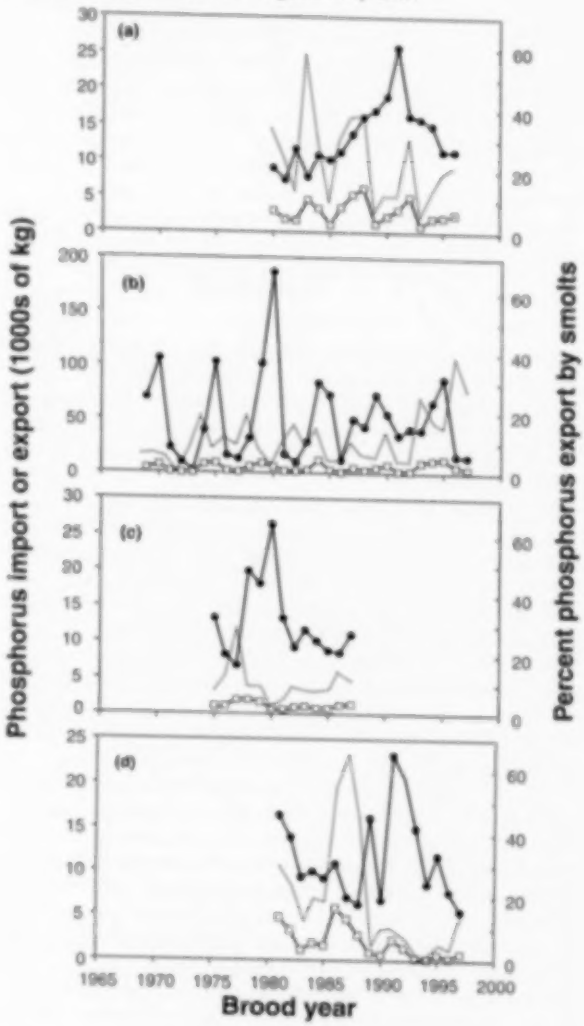

Fig. 2. Phosphorus import by adult sockeye salmon (*Oncorhynchus nerka*) (●) and export by sockeye smolts (□) by brood year in the Egegik (*a*), Kvichak (*b*), Wood (*c*), and Ugashik (*d*) river systems in Bristol Bay, Alaska. Note the different scales on the left-hand *y* axis. The import and export of nitrogen can be envisioned by multiplying the values for phosphorus by 7.9 for adults and 5.7 for smolts, their respective N:P ratios. The dotted line shows the percentage of parental nutrients that smolts export, corresponding to the right-hand *y* axis.

Smolts transported 10.5 ± 6.2% of this phosphorus and 7.6 ± 2.6% of this nitrogen each year, i.e., 1150 ± 441 kg of phosphorus and 6645 ± 2544 kg of nitrogen per year.

Returning sockeye transported 11 700 ± 5140 kg of phosphorus and 92 300 ± 40 600 kg of nitrogen each year to the Ugashik system. Smolts transported 19.2 ± 18.9% of this phosphorus and 14.0 ± 13.8% of this nitrogen each year from fresh waters to the ocean, i.e., 1980 ± 1760 kg of phosphorus and 11 428 ± 10 133 kg of nitrogen.

The percentage of parental nutrients that smolts exported, averaged across years for each system, was highly correlated

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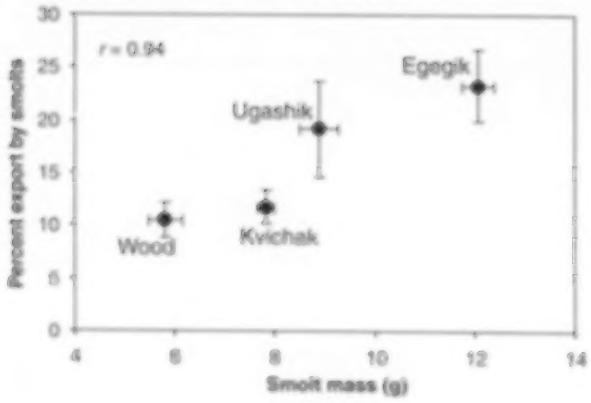
Fig. 3. Relationship between smolt body mass and the percentage of nutrients imported by spawners that smolts subsequently exported, averaged across all years of data (●). Error bars (±1 standard error) are shown for both smolt size and percentage exported to represent differences across years.

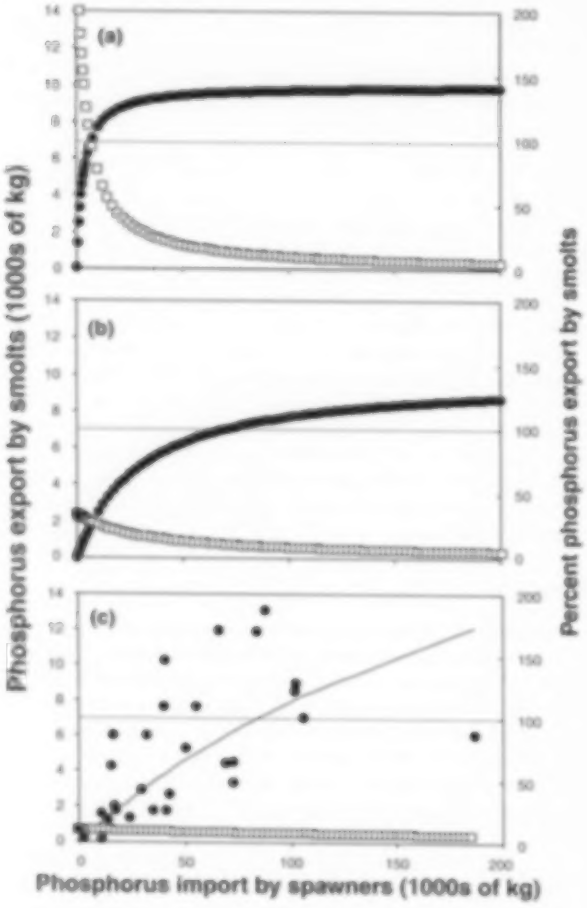


with the average smolt body size for that system (for phosphorus: Pearson's correlation, $N = 4$, $r = 0.94$, $P = 0.07$; Fig. 3), but was not significantly correlated with the average number of smolts per spawner (for phosphorus: Pearson's correlation, $N = 4$, $r = 0.625$, $P = 0.39$). The results for nitrogen were similar.

The percentage of the adult nutrients that smolts transported to the ocean varied not only from site to site but even more substantially through time (Fig. 2). In Egegik, smolts transported from 5.6% to 57% of the phosphorus and from 4.1% to 41.8% of the nitrogen their parents translocated from the ocean, while in Kvichak it ranged from 1.0% to 38.6% of the phosphorus and from 0.7% to 28.1% of the nitrogen. In Wood River, smolt transport ranged from 2.9% to 28.4% of the phosphorus and from 2.1% to 20.7% of the nitrogen, while in Ugashik it ranged from 1.3% to 64.7% of the phosphorus and from 0.9% to 47.1% of the nitrogen.

The percentage of parental nutrients that smolts export could also be influenced by the number of spawners and the degree of density-dependence that is characteristic of the system (Fig. 4). The two hypothetical stock–recruit (import–export) relationships that represented systems with intermediate and strong levels of density-dependence revealed that the lower the escapement (import), the higher the percentage of nutrients exported by out-migrating smolts (Figs. 4*a* and 4*b*). For example, with intermediate density-dependence, when spawners import less than 1000 kg of phosphorus to the system, smolts export 32% of the phosporus when they outmigrate. However, at large escapements, when spawners import, for example, 170 000 kg of phosphorus to the system, smolts subsequently export less than 5% of these nutrients. These differences are magnified even more in the case of strong density-dependence (Fig. 4*a*), where smolts export 8% of the phosporus imported by their parents when their parents imported 120 000 kg of phosphorus. However, when spawners import less than 7000 kg of phosphorus, smolts export more phosporus than their parents imported, and sockeye are acting as net exporters of nutrients from fresh waters rather than importers. The Beverton–Holt stock–recruit function described the Kvichak system reasonably well (negative log-likelihood = 31.8, $a = 30\,551$, $b = 283\,800$; Fig. 4*c*), but the relationships for the other three systems were poorly defined and thus are not presented. Using these parameters for Kvichak to predict nutrient export for a given level of import, smolts exported a relatively constant and low percentage of the nutrients their parents brought in (Fig. 4*c*). However, at lower escapements (lower import), smolts export a slightly higher percentage of the nutrients that their parents imported.

Fig. 4. Import–export (stock–recruit) relationships of phosphorus transport by sockeye for theoretical systems with strong (*a*) and intermediate (*b*) density-dependence. (*c*) Best-fitting import–export relationship for the Kvichak system (solid line) and the resulting percentage exported by smolts. Export by smolts for a given import by spawners is shown (●, corresponding to the left-hand *y* axis). The percentage of parental nutrients that smolts export is also shown (□, corresponding to the right-hand *y* axis). The broken line through 100% indicates when smolts export as much as spawners import.



Discussion

Sockeye transport large quantities of nitrogen and phosphorus from the ocean to freshwater ecosystems throughout Bristol Bay, Alaska. For example, in the Kvichak system, es-

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capement of sockeye transported, on average, 49 000 kg of phosphorus and 395 000 kg of nitrogen per year. Out-migrating smolts also transport large quantities of nitrogen and phosphorus. Smolts exported, on average, 16.2% of the phosphorus their parents exported. However, this average varied from 10.4% to 23.3% depending on the system, and varied from less than 1% to 64.3% depending on the year. From an alternative perspective, sockeye consistently act as net importers of nutrients to freshwater ecosystems, and, on average, spawners import over 6 times the phosphorus that their offspring export back to the ocean. Because the N:P ratio of adult sockeye was 73% higher than that of smolts, smolt consistently exported a smaller fraction of parental nitrogen than phosphorus.

To the best of our knowledge, there have been few studies in which nutrient transport by both smolts and adult salmon has been explicitly calculated. In his thesis on the phosphorus budget for Lake Iliamna (in the Kvichak system), Donaldson (1967) estimated that smolts removed 24.2% and 19.3% of the phosphorus that their parents brought in for the 2 years that he analyzed. These values are around twice as high as the average percent removal that we calculated for the Kvichak system. In addition, Naiman et al. (2002) calculated that smolts exported 6.7% of the cumulative nutrients that their parents had imported to Lake Iliamna, Alaska, over the last 40 years. This percent export is less than ours primarily because we calculated it on a brood-year basis and they averaged percent export of the nutrients that accumulated across all years. In addition, Stockner (1987) summarized the phosphorus budgets of five sockeye nursery lakes in Russia and the Pacific coast of North America, including quantifying phosphorus transport by adult and smolt sockeye. Using these phosphorus budgets, we calculated that smolt transport an average of 14.1% of the nutrients that their parents imported in these five lakes, and the percentage varied from 6.2% to 24.3%. Thus, in sockeye systems across the Pacific Basin, smolts consistently export from 5% to 25% of the nutrients that their parents import.

The percentage of parental phosphorus that out-migrating smolts export varies substantially among the four systems, from 10.4% for Wood River to 23.3% in Egegik. These differences between systems in the percentage of nutrients that smolts transport could be due to different numbers of recruits (smolts) per spawner, different sizes of out-migrating smolts, or the interaction between these factors. Although our statistical power was limited because we had data for only four systems, systems with larger smolts tended to have higher percentages of nutrient transport. For example, Egegik smolts export 23.3% of the phosphorus that their parents imported, around twice that exported by Wood River smolts (10.4%), and the Egegik smolts were around twice as heavy as the Wood River smolts (12.1 vs. 5.9 g). However, systems with higher numbers of outgoing smolts per spawner did not have significantly higher percentages of nutrient transport, perhaps because of strong density-dependence in smolt size at out-migration (e.g., Eggers and Rogers 1987).

There are several potential sources of error in our estimations of nutrient transport by smolt and adult sockeye. First, there is the potential for both human and instrumental errors in determining the numbers of returning adults and especially out-migrating smolts. Second, prior estimations of the nutrient content of salmon varied slightly. Any errors in the nutrient content or abundance of smolt and adult sockeye salmon would be linearly transferred to calculations of nutrient import and export. For example, changing a nutrient-content estimate by 1% of its value would lead to a 1% change in our calculation of net nutrient transport.

In the four sockeye systems in Bristol Bay, Alaska, that we examined, smolts exported an average of 16.1% of the nutrients that their parents imported. However, it is unclear how these calculations would compare with those from different systems with different species of salmon, different-sized smolts, different recruits-per-spawner relationships, and different ocean mortality rates. We predict that smolts will export a higher percentage of the nutrients their parents imported in systems with larger smolts, higher ocean mortality rates, and higher smolt production.

We investigated how nutrient export varies across different escapements with both our data and with hypothetical stock–recruit (import–export) relationships. The Kvichak system stock–recruit relationship was best defined by a Beverton–Holt relationship with a = 30 551 and b = 283 800, which produces very weak density-dependence in smolt production. However, if systems are characterized by stronger density-dependence, the percentage of parental nutrients that smolts export is often much higher at low spawner levels. Hypothetically, in systems that are characterized by extreme density-dependence, at low levels of escapement or nutrient import, smolts could actually export more nutrients than their parents import from the ocean. For example, if a pair of sockeye each weighing 2 kg produced 4000 eggs, and 15% of those survive to become smolts that averaged 10 g each, this pair of sockeye will have produced 6 kg of smolts. This pair of sockeye would have imported 15.4 g of phosphorus and 121.6 g of nitrogen while siring smolts that exported 25.9 g of phosphorus and 149.4 g of nitrogen. These size and egg-production values are within observed ranges (Burgner 1991).

Insight into the relationship between net import and net export can be gained by examining the parameters of the Beverton–Holt function in more algebraic detail (Fig. 5). By solving for import as a function of a and b, we can calculate the combinations of a, b, and import that will produce net import, net export, and a net balance of nutrient flux from fresh waters. If import is equal to export (smolts export 100% of the nutrients that their parents imported), then import is equal to parameter a minus parameter b. However, if import is greater than a minus b, then spawners import more than smolts export (net import) in systems with strong density-dependence in smolt production. Alternatively, if import is less than a minus b, then smolts export more than their parents imported (net export). Therefore, human activities such as fisheries that reduce escapement levels (import) could shift systems from a state where salmon act as net importers of nutrients to an alternative state where salmon act as net exporters of nutrients. Alternatively, human activities that cause decreases in smolt production could temporarily decrease the percentage of parental nutrients that smolts export from fresh waters, but this pattern would only be maintained if spawner numbers are not subsequently reduced.

This study quantifies gross fluxes of nutrients transported by sockeye between freshwater and marine ecosystems, but

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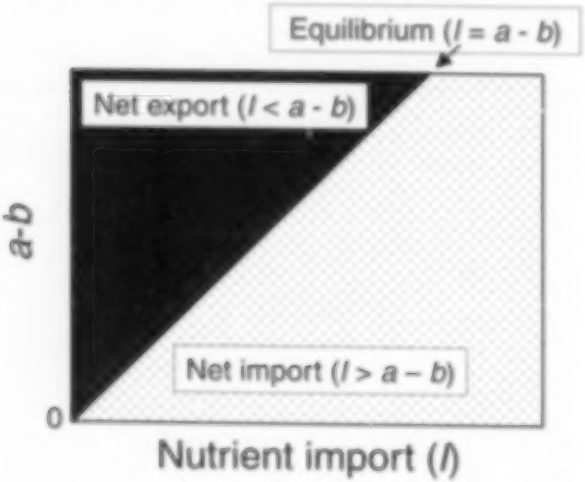
Fig. 5. Relationship between the Beverton–Holt parameters *a* and *b* fit to data in nutrient currency and net nutrient flux by salmon (*Oncorhynchus* spp.). The black region corresponds to situations where import (*I*) by spawners is less than the difference between parameters *a* and *b*, when salmon act as net exporters of nutrients. The stippled region corresponds to situations where import by spawners is greater than the difference between parameters *a* and *b*, when salmon act as net importers of nutrients.



does not attempt to track the pathways that these nutrients take or the impacts of the nutrients on the ecosystem. There is widespread evidence from analyses of stable isotopes that marine-derived nutrients accumulate in fresh waters (reviewed by Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). In previous studies it has been observed that when adult salmon migrate to fresh waters and die, the nutrients from their bodies are incorporated into a variety of ecosystem components: nutrients are incorporated directly via consumption by predators and scavengers such as grizzly bears (e.g., Hilderbrand et al. 1996) or juvenile coho salmon (e.g., Bilby et al. 1998), deposited into lake sediments (e.g., Donaldson 1967; Finney et al. 2000), or exported back into the ocean by hydrologic flows (e.g., Sugai and Burrell 1984) or smolts, or soluble fractions are taken up by periphyton or riparian vegetation (e.g., Helfield and Naiman 2001).

Returning salmon are only one of many sources of the nitrogen and phosphorus in fresh waters. Therefore, export of nutrients by out-migrating smolts, while composing a large fraction of the nutrients imported by adult salmon, comprises a smaller fraction of the total nutrient budget. However, returning adult salmon can be the dominant source of phosphorus in freshwater systems (Donaldson 1967) and a substantial source of nitrogen (Naiman et al. 2002). For example, according to Donaldson's (1967) phosphorus budget for Lake Iliamna, each year out-migrating smolts remove, on average, the equivalent of 6.6% of the phosphorus in the plankton, 1.7 times the phosphorus that is lost to sediments, and 29% of the phosphorus that leaves in the river outflow. It is likely that nitrogen export by out-migrating smolts is less ecologically important than phosphorus export, for two reasons: first, smolts export a smaller proportion of the nitrogen imported by their parents than of the phosphorus; second, these systems are generally phosphorus-limited, especially given the prevalence of nitrogen-fixing alder trees in these watersheds.

The pathways and impacts of the nutrients smolts transport from fresh waters to oceans are less well studied for smolts than for their parents. Juvenile salmon probably accumulate the majority of their nutrients from pelagic food webs in lakes, where they feed primarily on zooplankton (Burgner 1991). Thus, out-migrating smolts transport nutrients from the freshwater pelagic food web to marine ecosystems. Nutrients exported by smolts are probably incorporated into the marine food web as ocean-going salmon are eaten by birds, fishes, and marine mammals (reviewed by Burgner 1991).

In most previous studies of salmon-derived nutrients, nutrient transport by out-migrating smolts has been ignored (e.g., Larkin and Slaney 1997; Gresh et al. 2000) or assumed to be a small, constant fraction of the adult body mass. Our study has three important messages. First, out-migrating smolts can transport thousands of kilograms of nitrogen and phosphorus; in some years, a substantial portion of the nutrients that their parents brought in are taken back out to the ocean. Second, the percentage of adult nutrients that smolts transport to the ocean varies enormously across time and space, ranging from less than 1% to as high as 65%. Third, in systems characterized by strongly density-dependent stock–recruit relationships, smolts export a higher percentage of nutrients at lower escapements and in some circumstances could export more than adults. Therefore, human activities that reduce spawner numbers will not only reduce the raw import of nutrients (Larkin and Slaney 1997; Gresh et al. 2000), but also may increase the percentage of these nutrients that salmon smolts subsequently export back to the ocean, additionally decreasing net nutrient import to fresh waters by salmon. Furthermore, systems that are stocked with juvenile salmon but do not have naturally spawning adults may represent a case where anadromous salmon are acting as net exporters of nutrients from fresh waters. In the management of salmon-rearing systems, consideration should be given not only to the nutrients that adult salmon return to fresh waters, but also to the nutrients that smolts take away from fresh waters. Failure to do so will lead to consistent overestimation of the net amount of nutrients that anadromous salmon transport to fresh waters.

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Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers

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Abstract: The ability to traverse barriers of high-velocity flow limits the distributions of many diadromous and other migratory fish species, yet very few data exist that quantify this ability. We provide a detailed analysis of sprint swimming ability of six migratory fish species (American shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), striped bass (*Morone saxatilis*), walleye (*Stizostedion vitreum*), and white sucker (*Catostomus commersoni*)) against controlled water velocities of 1.5–4.5 $m \cdot s^{-1}$ in a large, open-channel flume. Performance was strictly voluntary: no coercive incentives were used to motivate fish to sprint. We used these data to generate models of maximum distance traversed, taking into account effects of flow velocity, body length, and temperature. Although the maximum distance traversed decreased with increasing velocity, the magnitude of this effect varied among species. Other covariate effects were likewise variable, with divergent effects of temperature and nonuniform length effects. These effects do not account for all of the variability in performance, however, and behavioral traits may account for observed interspecific differences. We propose the models be used to develop criteria for fish passage structures, culverts, and breached dams.

Résumé : Bien que la capacité de traverser des barrières de débits très rapides limite la répartition de plusieurs poissons diadromes et autres poissons migrateurs, il existe peu de données quantitatives sur le sujet. Nous présentons une analyse détaillée de la capacité de nage en sprint de six espèces de poissons migrateurs (l'alose savoureuse *Alosa sapidissima*, le gaspareau *Alosa pseudoharengus*, l'alose d'été *Alosa aestivalis*, le bar rayé *Morone saxatilis*, le doré *Stizostedion vitreum* et le meunier noir *Catostomus commersoni*) dans des courants de vitesse contrôlée de 1,5–4,5 $m \cdot s^{-1}$ dans une grande canalisation ouverte. La performance y était totalement volontaire; il n'y avait pas de stimulation coercitive pour pousser les poissons à la nage rapide. Ces données nous ont servi à mettre au point des modèles de la distance maximale traversée, en fonction des effets de la vitesse du courant, de la longueur du corps et de la température. Bien que la distance maximale traversée diminue avec l'augmentation de la vitesse du courant, l'importance de cet effet varie d'une espèce à l'autre. Les autres effets qui sont en covariation avec les premiers, comme les effets de la température et ceux des longueurs non uniformes, sont aussi variables. Ces effets n'expliquent pas, cependant, toute la variabilité de la performance; les caractéristiques comportementales expliquent peut-être les différences observées entre les espèces. Nous suggérons que nos modèles soient utilisés pour mettre au point des critères pour l'aménagement de passes migratoires de poissons, de canaux et de barrages comportant des brèches.

[Traduit par la Rédaction]

Introduction

Zones of high-velocity flow characterize many natural rivers and are often unavoidable, or even intentional, features of fishways, dams, and culverts (Clay 1995; Haro et al. 1998). These zones may constitute velocity barriers that exceed the physiological or behavioral capabilities of fishes and so define the upstream boundaries of their populations. The swimming performance of diadromous and other riverine fishes limits their ability to traverse these velocity barriers and is therefore central to their life history.

Many studies describe swimming endurance at sustained and prolonged speeds (for reviews, see Beamish 1978; Videler 1993), but few provide empirical measures of sprinting performance (throughout this text, we follow Webb's (1975) definition of sprinting as steady-state burst swimming). Of those studies that do measure sprinting performance (Beamish 1978), most are largely anecdotal, based on small sample sizes and collected under poorly controlled conditions. Even less common are studies that allow fish to volitionally ascend large-scale experimental open-channel flumes that more closely approximate natural conditions, allowing fish to express normal upstream migratory behaviors (for examples, see Dow 1962; Weaver 1963; Colavecchia et al. 1998).

Brett et al. (1958), Bainbridge (1958), and Beamish (1978) recognized the relevance of this information to improved fish passage and fishway design, but only Dow (1962) and Weaver (1963, 1965) quantified performance in units of the

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distance that fish were able to negotiate against a velocity challenge, the appropriate units for most applications. Weaver's (1963, 1965) work is exceptional, describing various aspects of swimming performance of thousands of individual salmon (*Oncorhynchus* spp.) and American shad (*Alosa sapidissima*) that entered his structure volitionally, with no handling and minimal human interference. Weaver's (1963, 1965) analyses were limited, however, to describing species-specific performance during fixed-velocity tests and gave only cursory treatment to covariates such as length and temperature. Moreover, hydraulic conditions varied down the length of his flume apparatus, complicating interpretation of his results.

Although the techniques used by Dow (1962) and Weaver (1963, 1965) provide close approximations to conditions fishes encounter in nature, most studies on swimming performance have followed the approach of Brett (1964) in which fishes swim against carefully controlled flow within enclosed chambers. None of these studies has matched the scale of Weaver's (1963, 1965) work, however, and the ability of fish to traverse velocity barriers has remained poorly quantified.

The lack of information on sprinting performance is problematic for the design of structures for passing fish around dams and other obstacles. Most fishway manuals (e.g., Powers et al. 1985; Bell 1991; Clay 1995) use figures presented by Beach (1984) to estimate maximum swimming capacities. Beach's (1984) models were derived from the swimming energetics of sockeye salmon (*Oncorhynchus nerka*) (Brett 1965), in vitro muscle kinematics data (Wardle 1975, 1980), and numerous assumptions, including homogeneity of glycogen stores across populations and taxa. Clearly, these models do not support the breadth of their current application. Moreover, they do not predict traversable distance through velocity barriers, only maximum swim speeds and expected endurance. If maximum sprinting ability is underestimated (and this may often be the case (Videler and Wardle 1991)), then some fish passage designs could be simplified, facilitating mitigation efforts and making available much-needed habitat.

The value of low-cost mitigation efforts is not trivial. A recent inventory identifies more than 77 000 dams greater than 8 m throughout the United States, and smaller structures that also impede passage of anadromous and riverine fishes are even more numerous (US Army Corps of Engineers 2001). Similar densities of riverine obstructions can be found throughout the developed world (e.g., several references in Jungwirth et al. 1998). Of the lower-head structures, many are nonfunctional or in disrepair and could be easily breached to form routes of passage, provided that fishes are capable of traversing the resulting velocity barriers (Odeh 1999).

Because of the lack of detailed information on sprinting performance, however, engineers and managers often are unable to assess whether species of concern will be able to pass such simple structures as breaches, culverts, etc. Existing manuals for fish passage engineers provide scant estimates of instantaneous maximum sprint speeds and no estimates of sprint distances through high-velocity flow (e.g., Bell 1991; Clay 1995). The need for reliable data on volitional fish swimming performance is increasing as fish passage issues and concerns expand to include riverine species that are not anadromous but that may regularly migrate considerable distances throughout a watershed. Relatively little is known about swimming performance of these species.

In this study, we provide a detailed description and analysis of high-speed swimming performance (i.e., prolonged and sprint modes) by six species of anadromous, amphidromous, and potamodromous fishes commonly found in rivers of eastern North America. We present species-specific models of maximum ascent distances of fish swimming against steady, open-channel flow velocity conditions ranging from 1.5 to 4.5 $m \cdot s^{-1}$. These data will help identify distributional limits and can also be used to design and evaluate new and existing passage structures or, conversely, to create velocity barriers for nuisance species.

Methods

Flume apparatus

To simulate conditions found at natural and anthropogenic velocity barriers, we built a large open-channel flume (1 m width × 1 m depth × 24 m length, zero slope) in the S.O. Conte Anadromous Fish Research Laboratory fish passage complex (Fig. 1) located at Turners Falls, Massachusetts, next to the Connecticut River. The flume was constructed of a wood and steel frame, with the floor and one wall made of plywood. The opposite wall was made of 2.5-cm-thick clear acrylic sheet. Mirrors installed at a 45° angle to the transparent wall permitted simultaneous side and top views to video cameras arrayed above the flume. The plywood wall and floor were covered with white retroreflective material (3M Corp.) (Scotchlite 6780) on which reference marks (black crosses 10 cm × 10 cm) were painted at 0.5-m (horizontal and vertical) intervals. To prevent the formation of organized eddies (macroturbulence), the floor and walls were made smooth, straight, and level. To ensure uniform lighting and to block sunlight from the skylights of the fish passage complex, a black tarp was laid out on a grating 4.5 m above the flume, covering its full length, and the flume was illuminated with eight 90-W halogen flood lamps.

Ambient river water was supplied to the flume from an adjacent hydroelectric power canal fed by the Connecticut River. Water entered the fish passage complex through a 1.8-m-diameter pipe into an upstream diffusion chamber to the test flume head pond. Water from the head pond entered the test flume through an electronically actuated sliding gate (head gate) and exited the flume into a downstream staging area (8 m long × 3 m wide × 0.60–1.35 m deep). Mean velocities were slower in the staging area because of its greater width and depth, the latter being controlled by a variable-height weir (tail-water weir) at the downstream end. This weir was fitted with a screen to retain fish in the staging area while allowing water to pass through. After passing over the tail-water weir, water was returned to the river downstream of the fish passage complex through a 1.4-m-diameter pipe. Water velocities within the flume were controlled by the head-pond level, the head-gate opening, and the tail-water weir level.

We used a 1:6 scale physical model of the flume to establish experimental hydraulic test conditions. The model was constructed to be geometrically, kinematically, and dynami-

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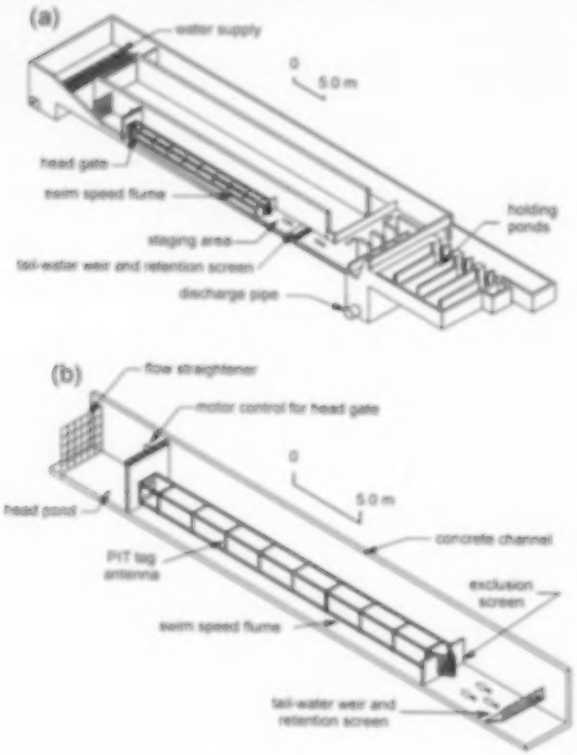
Fig. 1. Fish passage complex at the S.O. Conte Anadromous Fish Research Center. (*a*) Installation of swimming speed flume showing holding ponds and route of introduction for test fish; (*b*) detail of swimming speed flume showing flow control mechanism and arrangement of PIT tag antennas.



cally similar to the full-scale flume, ensuring identical hydraulic characteristics (Chow 1959). The model was used to identify the gate settings and water surface elevations in the head pond, flume, and staging area that characterized four test velocities (U_t; nominally 1.5, 2.5, 3.5, and 4.5 m·s^{-1}) and to quantify the response of flow velocity within the flume to variations in these conditions.

Open-channel flow is characterized as super- or subcritical, depending on whether velocities are dominated by inertial or gravitational forces, respectively. The Froude number, F, which equals the ratio of these two forces, identifies the state of flow:

$$(1) \qquad F = \frac{U_t}{\sqrt{gL}}$$

where g is gravitational acceleration and L is the depth of flow in a channel with a rectangular cross section (Chow 1959). Flow is supercritical at $F > 1$ and subcritical at $F < 1$. At $F = 1$, the flow is critical, and a standing gravity wave (or hydraulic jump) may be propagated up the length of the flume (e.g., Weaver 1963). These unsteady flow conditions were unacceptable for this study, so depth of flow was varied to maintain either super- or sub-critical conditions over the full length of the flume.

At 1.5 m·s^{-1}, flow in the test flume and staging area was subcritical and was set at a depth of 96 cm. At higher velocities, however, this depth of flow created excessive velocity and turbulence in the staging area. Reducing the depth lowered the total flow within the flume, thus maintaining a quiescent staging area. Velocity was sufficient under the 3.5 and 4.5 m·s^{-1} conditions to maintain supercritical flow down the length of the flume at about 45 cm depth. At 2.5 m·s^{-1}, however, flow was unstable and became critical midway down the flume at this depth, so depth was reduced to 26 cm at this velocity to maintain the supercritical condition. For each of these supercritical conditions, tail-water depth was greater than the depth of flow within the flume and was set such that a hydraulic jump was maintained within the flume 0.5–1.0 m from the downstream entrance.

Detailed velocity measurements were made in the model to describe the flow field through which fish would swim. A two-directional electromagnetic velocity meter (Marsh-McBirney model 523) with a 13-mm probe was used to measure model velocities; actual velocities were then measured throughout representative cross sections of the full-scale flume on a 5-cm grid using a propeller meter (Ott model 1-113040). Two-dimensional flow velocity profiles were generated for 1.5, 2.5, and 3.5 m·s^{-1} trial conditions, respectively (Fig. 2). We were unable to collect similar data for the 4.5 m·s^{-1} condition because of excessive forces on the velocity probe; however, hydraulic principles dictate that the velocity profile will be similar to that of the 3.5 m·s^{-1} condition (Chow 1959). To characterize the turbulence of the flow, three-dimensional velocities were measured in the model using a 3D SonTek acoustic doppler anemometer. Measurements were made at mid-depth, both at the center and at distances equivalent to 12.7 cm from the wall of the full-scale flume and 12 m from its downstream end.

Data collection

We used an automated passive integrated transponder (PIT) system to record the position of fish swimming up the length of the flume. Fish were externally tagged without anaesthesia by bonding PIT tags (32 mm in length, 3.9 mm in diameter) to a small fishhook, which was inserted into the cartilage at the base of the dorsal fin (second dorsal in the case of percomorphs; see Castro-Santos et al. (1996) for a description of the PIT system, tagging method, and its application). Ten PIT antennas were mounted along the length of the flume at 2.5-m intervals (from 0.5 to 23.0 m); of these, eight were in place for the first half of the study, and two more were added in May 1998. Tags were detected within 0.5 m of the plane of each antenna loop. A control computer logged tag detection data (tag code, date, time to the nearest 0.1 s, and antenna location) from PIT readers.

Fish were collected and tested during the period from April through July 1997–1999. Six species of migratory fishes were captured from traps at nearby fishways (American shad (*Alosa sapidissima*), striped bass (*Morone saxatilis*), and white sucker (*Catostomus commersoni*)) and coastal streams (alewife (*Alosa pseudoharengus*) from the Herring River, Bourne, Massachusetts, and blueback herring (*Alosa aestivalis*) from the Charles River, Watertown, Massachusetts) or electrofished (blueback herring, striped bass, walleye (*Stizostedion vitreum*), and white sucker from the

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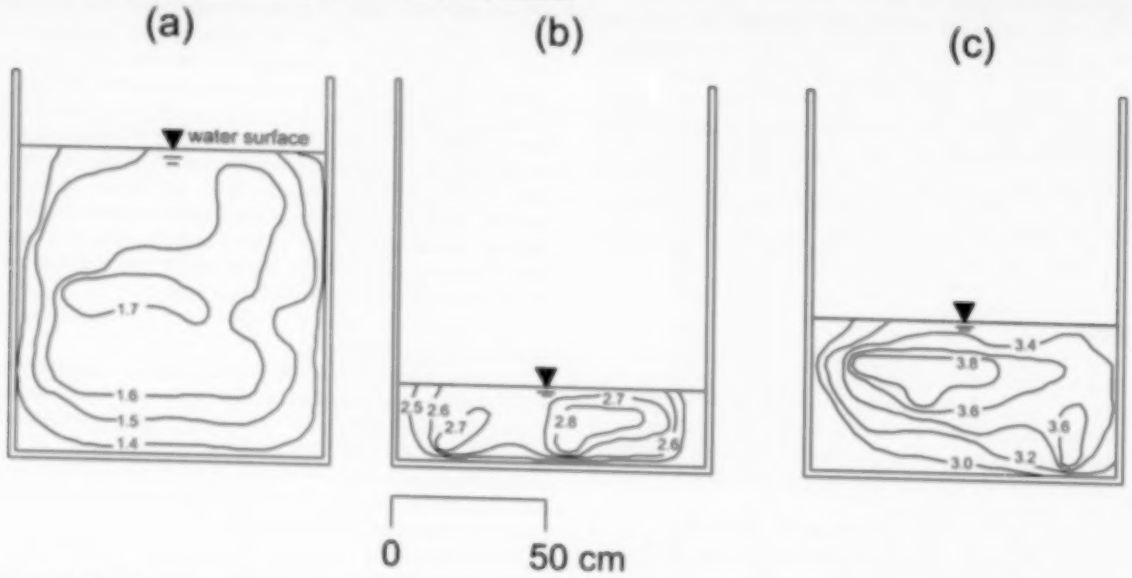
Fig. 2. Cross-sectional velocity profiles ($m \cdot s^{-1}$) of swimming speed flume under nominal (*a*) 1.5 $m \cdot s^{-1}$, (*b*) 2.5 $m \cdot s^{-1}$, (*c*) and 3.5 $m \cdot s^{-1}$ mean water velocity conditions 2 m upstream of the flume entrance.



Connecticut River) on dates corresponding to the periods of upstream migration for each species. Fish were transported to the flume facility in one of two truck-mounted tanks (1000 and 4000 L capacity). After transport, fish were measured (fork length), sexed, and fitted with a PIT tag (Castro-Santos et al. 1996); we assume that this very small tag had no substantial effect on swimming performance. Fish were transferred into open, flow-through holding ponds (Burrows and Chenoweth 1970) that were hydraulically continuous with the fish passage complex and held 24 h before testing. Fish were usually tested within 24 h of capture and were released after each trial. In some cases, fish were held longer before testing, but never for more than 7 days.

At the start of a trial, groups of 20–30 fish were seined from the holding ponds into the staging area, and the tailwater weir and screen were raised to confine the fish to this area. Fish were initially prevented from entering the flume by an exclusion screen. Once the water velocity in the flume was brought to the desired level, the exclusion screen was opened and fish were allowed to ascend the flume of their own volition. Only those fish that entered the flume during a given trial were included in our analyses. Although duration of runs ranged from 1 to 6 h, we use only the first hour's data from each trial to maintain consistency in our analyses.

Light level in the flume was 2.5 $\mu W \cdot m^{-2}$ for all species except walleye and white sucker. To encourage attempts by these species, which typically migrate at night, we darkened the flume to 0.03 $\mu W \cdot m^{-2}$. Mean hourly water temperatures were logged using a data logger (Licor LI-1000) and thermocouple probe (Omega T-type). Average temperatures for times corresponding to each trial were included as a covariate in the analyses.

Data analysis

Because the PIT antennas effectively graduated the flume into 2.5-m intervals, we were able to estimate maximum distance of ascent (D_{max}) by selecting the location farthest upstream that was logged for each fish during the trial. This is an incremental measure and provides a conservative bias to the D_{max} estimate: the reader might detect a fish as far as 0.5 m below an antenna, but the same fish could also be as much as 2 m above that antenna without being logged at the next location.

The configuration of the PIT antennas imposed restrictions on the methods used to develop predictive models. Since PIT antennas were installed only for the first 18 m of the flume during the first half of the study, and the first 23 m thereafter, D_{max} values do not reflect the true maximum ability of the fish, but rather the maximum that our apparatus was able to measure — the actual performance capacities may have been higher. This condition, in which the magnitude of a measured variable exceeds the ability of an instrument to measure it, constitutes censoring (Lee 1992). Ordinary least-squares regression techniques are unable to accommodate censoring, so we applied the maximum likelihood regression techniques commonly used in survival analysis (Allison 1995; Castro-Santos 2002; Castro-Santos and Haro 2003) to develop our predictive models. For the reasons just described, as well as to negate any effect of fish avoiding the upstream end of the flume, fish attaining D_{max} values of 18 m or greater were included in the analyses as censored observations.

The regression models used here follow the form

$$(2) \qquad (\ln D_{max})_p = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k + w_p$$

where $(\ln D_{max})_p$ is the pth quantile of the natural log of D_{max}, βs are coefficients, x_is are the k-covariates, and w_p is the pth quantile of the baseline distribution. One advantage of this regression approach is that it does not require the error term to be normally distributed. For this reason, it takes on a more complex structure than that of ordinary least-

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squares regression, with scale (σ) and shape (δ) parameters that influence the value of w_p.

We determined which distribution best described our data by first including all three covariates: velocity, temperature, and body length. We then generated separate models based on exponential, lognormal, Weibull, log-logistic, and generalized gamma distributions (Lawless 1982) as well as their nonlogged counterparts. Next, we ranked these models using Akaike's information criterion and selected the one with the best fit (Allison 1995; Burnham and Anderson 1998). Finally, we refined the models by removing covariates in a stepwise fashion, retaining only those with P values less than 0.15.

Results

Flume hydraulics and tolerances

Mean velocities differed consistently from the projected nominal velocities (Table 1). Test velocities varied little, with most standard deviations less than 0.1 m·s^{-1}. This variability arose primarily as a result of fluctuating head-pond levels in the power canal.

Flow is either laminar or turbulent depending on its Reynolds number, R. This is the ratio of inertial to viscous forces:

$$(3) \qquad R = \frac{U_f d}{\nu}$$

where d is a characteristic length (in this case, the cross-sectional area divided by the length of its wetted perimeter) and ν is the kinematic viscosity of the working fluid. Open-channel flow becomes turbulent at $R > 2500$ (Chow 1959). Under all of the velocity and depth conditions used here (Table 1), $R > 300\,000$, well within the turbulent regime.

Turbulence is typically quantified by the standard deviation of the velocity vector (u') or alternatively by its coefficient of variation (CV) or relative turbulence intensity:

$$(4) \qquad \mathrm{CV} = u'/\bar{U}_f$$

where $\bar{U}_f$ is the mean channel velocity. In geometrically similar channels, turbulence scales directly with velocity, regardless of Froude and Reynolds numbers, and so its CV is constant (Nezu and Nakagawa 1993). The acoustic doppler anemometer data indicated that turbulence intensity within the flume was 0.11–0.17, which is characteristic of open-channel flow over smooth surfaces. The turbulence was disorganized, however, consisting of random fluctuations and microeddies with no evident periodicity (Fig. 3) (Nezu and Nakagawa 1993). The measured level of turbulence in our flume was representative of flows through long open channels (i.e., culverts, dam notches) but less than that within technical pool and weir and Denil-type fishways.

Velocities were lowest near the walls and floor of the flume (Fig. 2) and were within 10% of the mean cross-sectional velocity throughout its length. However, assertions that fish will consistently seek out zones of lowest velocity (e.g., Beamish 1978; Pavlov et al. 2000) were not borne out by our observations. Although some species (most notably white suckers) actively selected these low-velocity zones at the 1.5 and 2.5 m·s^{-1} conditions, all species swam near the cross-sectional center of the flume at the higher velocities (Castro-Santos 2002).

The presence of the hydraulic jump 0.5–1.0 m from the flume entrance under the supercritical flow conditions may have provided some advantage to the fish, particularly at higher velocity flow, allowing them to ascend the first half metre with greater ease than they would have had the jump been outside the flume. The jump was kept within the flume to reduce the strength of the jet issuing into the staging area and to help encourage fish to enter the flume. Researchers seeking to replicate our results should maintain similar conditions; those seeking to predict ascent distances at field sites should measure from 1.0 m below the hydraulic jump in conducting their calculations.

Swimming capacity

Because impingement of smaller species (alewife, blueback herring, and walleye) on the tail-water weir screen occurred in initial 4.5 m·s^{-1} trials, and because performance was poor under the 3.5 m·s^{-1} condition (Fig. 4), these smaller species were not run at 4.5 m·s^{-1}. Percentages of fish entering the flume varied both among species and among velocities within species (Table 1).

Increasing water velocity consistently reduced D_{max} for each species (negative β, Table 2). Coefficients indicate the relative effect of each covariate on log distance of ascent, i.e., each unit increase in covariate results in an increase in distance of $100 \times [1 - \exp(\beta)]$ percent. Thus, although all species showed the expected negative effect of water velocity on D_{max}, the degree of this effect varied widely among species (e.g., 49% decrease in distance per metre per second for walleye versus a 69% decrease for blueback herring).

Body lengths and temperatures (Table 1) represent values typical for active migrants of these species in our region (northeastern United States). Blueback herring and alewife had the smallest size ranges (45 and 55 mm, respectively) followed by American shad and walleye (195 mm each) and white sucker (220 mm). Our walleye sample, however, did not include the largest individuals present in the adult migratory spawning population (this was to accommodate concerns of local fisheries managers). Striped bass, in contrast, showed the greatest size variability of all (735 mm). This is because upstream migration of striped bass includes both juvenile and spawning individuals, so the tested fish of this species are not necessarily mature adults.

Performance improved significantly with length for American shad, blueback herring, striped bass, and walleye. This effect varied over an order of magnitude, being least for American shad and greatest for blueback herring. However, over the range of lengths represented by ±1 SD, the predicted effect on D_{max} was greatest for striped bass (277% increase in D_{max} from small to large individuals) and least for American shad (16% increase), with 60% and 36% increases among blueback herring and walleye, respectively. Note that the narrow scope of sizes of blueback herring means that these data should be viewed with caution.

Trial temperatures reflected ambient river conditions. Alewife experienced the narrowest temperature range (4.7 °C) and white sucker and striped bass the largest (12.4 and 13.6 °C, respectively). Trials of the remaining species had similar temperature ranges (8.3–8.5 °C). These temperature

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Table 1. Species characteristics, sample sizes, and hydraulic conditions of tests performed in the swimming flume by nominal water velocity, all years pooled.

					Hydraulics			
Species	*N*	%	Fork length (mm)	Temperature (°C)	Nominal velocity ($m \cdot s^{-1}$)	Measured velocity ($m \cdot s^{-1}$)	Water depth (m)	*Q* ($m^3 \cdot s^{-1}$)
American shad	92	86	421±34 (355–495)	16.8±1.5 (15.3–19.1)	1.5	1.74±0.07	0.96	1.67
	233	68	417±33 (355–495)	18.9±2.1 (13.4–21.6)	2.5	2.69±0.09	0.26	0.70
	285	71	415±36 (325–520)	18.4±2.0 (13.4–21.5)	3.5	3.43±0.09	0.45	1.54
	92	33	416±35 (350–510)	18.2±2.4 (13.3–21.5)	4.5	4.53±0.04	0.46	2.08
Alewife	122	55	235±12 (210–265)	10.2±1.4 (8.5–13.2)	1.5	1.60±0.15	0.96	1.54
	60	30	238±11 (215–265)	10.4±1.4 (8.9–13.0)	2.5	2.60±0.06	0.26	0.68
	40	37	235±11 (215–260)	11.2±1.4 (9.1–13.0)	3.5	3.40±0.03	0.45	1.53
Blueback herring	19	17	229±11 (210–245)	16.7±2.3 (13.2–18.2)	1.5	1.61±0.09	0.96	1.55
	24	18	219±11 (205–245)	16.7±3.4 (13.0–21.4)	2.5	2.69±0.07	0.26	0.70
	38	34	216±11 (200–240)	17.1±2.4 (13.0–20.6)	3.5	3.40±0.13	0.45	1.53
Striped bass	10	33	558±270 (290–970)	18.6±0.0 (18.6)	1.5	1.58±0.05	0.96	1.52
	57	38	430±118 (235–780)	19.9±2.7 (16.3–23.6)	2.5	2.64±0.07	0.26	0.69
	62	33	478±120 (280–760)	19.3±2.8 (10.7–24.3)	3.5	3.40±0.06	0.45	1.53
	48	70	554±162 (285–833)	17.2±1.3 (16.2–21.9)	4.5	4.55±0.09	0.46	2.09
Walleye	13	24	314±45 (240–395)	12.6±2.5 (9.3–14.4)	1.5	1.74±0.11	0.96	1.67
	24	30	315±41 (270–410)	15.7±3.4 (10.0–17.8)	2.5	2.73±0.11	0.26	0.71
	12	22	317±53 (225–415)	10.3±0.7 (9.7–11.1)	3.5	3.34±0.01	0.45	1.50
White sucker	35	65	385±41 (285–505)	11.8±0.9 (10.9–14.4)	1.5	1.75±0.05	0.96	1.68
	35	41	384±29 (305–430)	14.9±3.6 (11.0–18.4)	2.5	2.62±0.05	0.26	0.68
	31	36	392±30 (340–450)	17.6±5.6 (10.7–22.8)	3.5	3.36±0.03	0.45	1.51
	31	49	398±26 (340–450)	15.0±3.6 (10.4–21.5)	4.5	4.51±0.04	0.46	2.07

Note: Sample size (*N*) is presented as total number of fish entering the flume followed by the percentage that this represents of the total number of fish introduced into the staging area. Lengths, temperatures, and measured velocities are given as means ±1 SD; length and temperature ranges are in parentheses. *Q* is the total flow within the flume.

ranges should have been sufficient to detect any effect of temperature on performance. This effect, however, was ambiguous. Performance increased with temperature for blueback herring, walleye, alewife, and striped bass (although the effect was nonsignificant for the latter two species) but decreased with temperature among American shad.

Duration of holding times before testing varied because the timing of trials was contingent on availability of fish. Although 89% of fish were tested within 48 h of capture, some collections, most notably among white sucker, were held for as long as 7 days before testing. Inclusion of this factor in the regression models (Table 2) indicated that holding time had no significant effect on D_{max} for any of the species tested ($P > 0.07$ among walleye, $P > 0.42$ for all others). Likewise, collection point and method did not substantially affect D_{max} ($P > 0.19$).

The distributions that best describe the performance data differed among species (Table 2). The gamma distribution provided the best fit to the data for American shad, alewife, striped bass, and walleye; the Weibull distribution best described the blueback herring and white sucker data. The scale (σ) and shape (δ) parameters of the regression models describe the shape of the underlying error distribution. Evaluation of probability plots (SAS Institute Inc. 1999) and Cox–Snell residuals (Allison 1995) suggests that these models provide a reasonable fit to the data.

The purpose of the regression models (Table 2) is not only to identify significant factors influencing swimming performance but also to quantify these effects in a way that enables managers and engineers to apply our data to similar hydraulic environments. By setting covariate values to levels representative of specific situations, managers can use these models to predict proportions of populations able to pass barriers under various velocity conditions (Fig. 5). Proportions can be estimated for each model as Weibull

$$S(D) = \exp\left[-\exp\left(\frac{\omega - \mu}{\sigma}\right)\right] \quad (5)$$

and gamma

$$S(D) = \frac{\Gamma\left\{\delta^{-2}, \delta^{-2}\exp\left[\delta\left(\frac{\omega - \mu}{\sigma}\right)\right]\right\}}{\Gamma(\delta^{-2})} \quad (6)$$

where the survivorship function $S(D)$ is the proportion of fish successfully passing a velocity barrier of distance D, $\omega = \ln(D)$, σ is the the scale parameter, δ is the the shape parameter, $\Gamma(a)$ and $\Gamma(a,b)$ are the complete

$$\Gamma(a) = \int_0^\infty D^{a-1}\exp(-D)\mathrm{d}D \quad (7)$$

and incomplete

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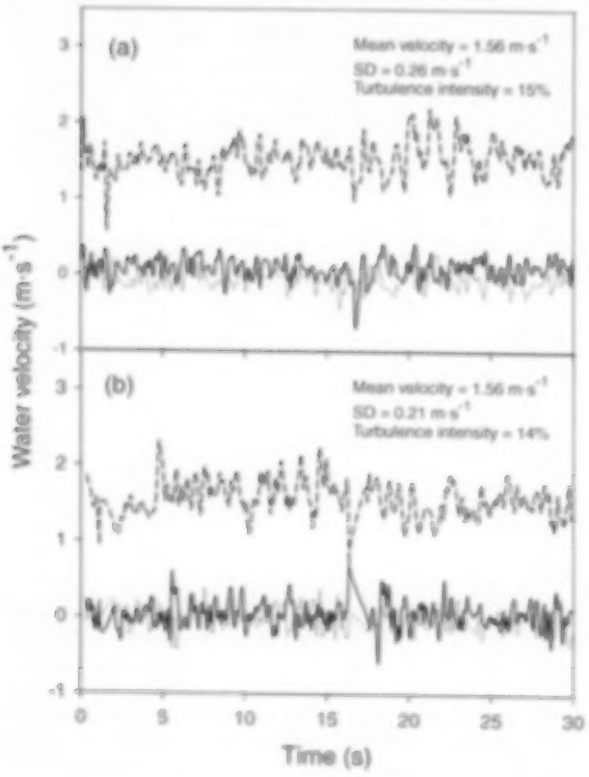
Fig. 3. Time series of three-dimensional water velocity within the flume apparatus at 1.5 m·s^{-1} nominal velocity 12 m upstream from the flume entrance and 50 cm from the floor at positions (*a*) near the side wall and (*b*) at the flume midline. Dashed line, *X* velocity; solid line, *Y* velocity; dotted line, *Z* velocity.



$$\Gamma(a,b)\int_0^{\infty} D^{a-1}\exp(-D)\mathrm{d}D \quad (8)$$

gamma functions, respectively (Lawless 1982), and $\mu = \mathbf{X}\boldsymbol{\beta}$, the vector product of covariate values and their coefficients.

Discussion

Current criteria for the design of fishways and velocity barriers are based on biological data collected under very artificial conditions. Often, these conditions are a necessary feature of controlled laboratory studies. For example, respirometry studies require a uniform flow profile to prevent fish from taking advantage of low-velocity zones. Also, fish are typically required to swim within enclosed tubes, and it is not known how representative the resulting data are of natural situations. Our data represent a departure from and improvement over these methods: fish swam volitionally in open-channel flow, and D_{max} values represent behavioral rather than explicitly physiological fatigue.

Our results can be readily compared with published direct measures of sprint swimming and distance ascended. Weaver (1965) measured a median distance of ascent of 9.4 m for American shad at a flow velocity (U_f) of 3.47 m·s^{-1} and of 5.94 m at a U_f of 4.02 m·s^{-1} (temperature 20.8 °C, fish lengths not given). For comparable U_f values, temperatures, and a mean fork length of 417 mm, our model predicts 50% passage at 10.1 and 5.9 m (respectively) for American shad. It is also interesting to note that Weaver's (1965) estimates of sprint swimming performance of adult Pacific salmonids greatly exceeded that of any of our test species. Thus, our data do not conflict with previous observations of swimming performance of salmonids; rather, they point to superior swimming performance measured in open-channel flow. Dow (1962) and Stringham (1924) observed alewives swimming in open-channel flows against velocities of 3–4.5 m·s^{-1}, but their data were poorly quantified. Because we did not directly measure relationships between swimming speed and fatigue time, our data do not readily compare with most published information on these metrics. However, we did observe that many fish swam at speeds of 10–20 body lengths·s^{-1} (Castro-Santos 2002), which are well above those measured by earlier investigators employing forced swimming techniques (Beamish 1978; Videler 1993).

There are, however, limits to the application of our data. Natural rivers, fishways, and culverts often have roughness elements, weirs, or objects in the flow that impart structure to the turbulence (macroeddies). In some situations, fish are able to use this structure to assist their forward movement (Hinch and Rand 2000; Pavlov et al. 2000) or station holding abilities (Webb 1998; Liao et al. 2003*a*, 2003*b*). In other situations, turbulence structures can hinder these same behaviors (Hinch and Rand 1998; Webb 1998). Because our flume was an open channel, with smooth walls and floor, the turbulence was characterized by microeddies (much smaller than the length of a fish), which can be expected to increase the cost of swimming (Enders et al. 2003). Thus, the models presented here should be applied only to those situations that are hydraulically similar to our laboratory conditions. Examples include box culverts, breached dams (with minimal structure in the flow), and zones of supercritical flow within fishways. The models may reasonably provide guidance for situations that deviate moderately from those presented here, such as culverts with corrugated roughening elements. Also, some fishway types (e.g., Alaska steeppass) are characterized by zones of axial flow surrounded by zones that are more turbulent (Odeh 2003). If fish ascend these fishways using the less turbulent zones, then the models presented here may have some relevance. Application to any such situation should be viewed with skepticism, unless information on the behaviors of the fish is available to justify it. Future work should focus on providing detailed descriptions of the behaviors of fish traversing zones of turbulent flow, characterizing the turbulence, and identifying those conditions that act to increase or decrease D_{max}. The methods described here can serve as a model for this work.

Because we constructed the flume to be of such a length as to provide realistic estimates of passage ability past obstacles of relatively short length (e.g., breached low-head dams), some individuals could successfully negotiate the full length of the flume, particularly at the lowest velocities. Other places where high velocities exist, such as culverts, natural obstructions, etc., may extend well beyond the length of our structure, and our data may have limited relevance to such situations. Using the survival analysis approach, our data al-

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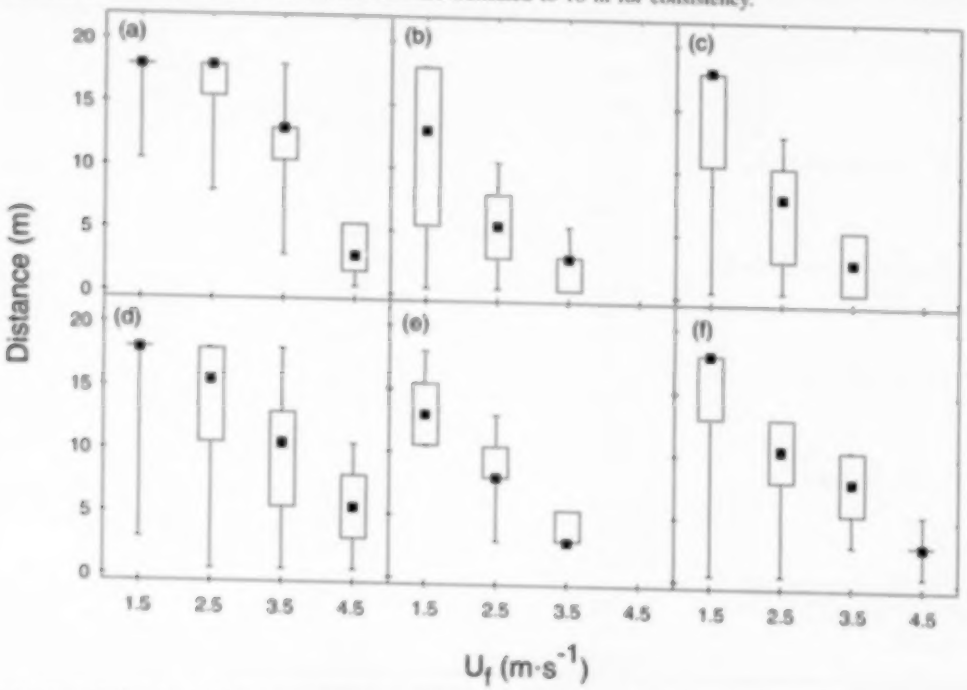
Fig. 4. Maximum distance of ascent (D_{max}) by species and nominal water velocity (U_f). (*a*) American shad; (*b*) alewife; (*c*) blueback herring; (*d*) striped bass; (*e*) walleye; (*f*) white sucker. Data are presented as median (■), 25–75 percentiles (boxes), and 5–95 percentiles (whiskers). Note that actual water velocities deviated from nominal velocities. Smaller species (alewife, blueback herring, and walleye) were not run against the 4.5 m·s^{-1} condition. Data are truncated to 18 m for consistency.



low for modest extrapolation beyond the actual length of the flume and for interpolation between and extrapolation beyond the experimental test velocities (Hosmer and Lemeshow 1999). We recommend limiting such extrapolations to velocities of 0.5 m·s^{-1} greater or less than the test velocities and total distances of 25 m. These values are similar to those required for interpolation between test conditions and antenna locations; extrapolation beyond these limits is not justified. It should be noted, however, that at lower speeds, fish might shift to prolonged, or even sustained, mode (Webb 1975). These modes are characterized by different swim speed – fatigue time relationships, and estimates of D_{max} based on sprint data can be expected to be low (Castro-Santos 2002).

Keeping in mind that caution should be used when applying these equations to situations much different from our experiments, the following example might help elucidate their application. To estimate the proportion of 50-cm striped bass passing a 10-m-long velocity barrier of 3.0 m·s^{-1} flow at 18 °C, values from Table 2 are entered into eq. 6 to generate an estimate of 65.9% passage through this barrier. A similar process could be used to describe a population with a range of sizes by breaking it down into more meaningful ranges (e.g., by age class).

Few studies of unsustained (i.e., prolonged and sprint) swimming performance have been conducted on this scale, and this is the first to quantify performance in terms of distance traversed against controlled open-channel velocity barriers with such resolution and large sample sizes and on such a range of taxa. Weaver (1963, 1965) provided empirical quantile curves for American shad, steelhead (*Oncorhynchus mykiss*), chinook salmon (*Oncorhynchus tshawytscha*), and coho salmon (*Oncorhynchus kisutch*) but did not rigorously evaluate effects of temperature, fish length, or flume hydraulics. Other efforts have focused on timing the movements or recording the success of individuals ascending fishways (Dow 1962) or on angled fish running out a line attached to a tachometer (Gero 1952). All of these approaches have been done under poorly controlled conditions or failed to gather detailed individual information.

As a result of the large sample sizes and individual information that we were able to collect, we could construct models that accurately describe the shapes of probability functions, thus permitting realistic estimates of percentiles of populations capable of passing barriers of specific velocities. This allows for the ability to target for passage of a particular proportion of the population, which is an improvement over use of means and medians that only describe midpoints for proportion of fish passed and do not account for variability (Venditti et al. 2000; Castro-Santos and Haro 2003).

One caveat to consider when applying these data is that we do not include all fish in our analyses, only those that initiated attempts within 1 h. This was done to eliminate the effect of motivation or attraction (quantified in this study by the percentage of fish entering the flume from the staging area), which differed nonlinearly between velocities (Castro-Santos 2002). Thus, our models are conditional on the fish staging attempts and may not be representative of those achievable by fish that made no attempts to ascend the

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Table 2. Regression models of covariate effects on log maximum distance of ascent (ln (D_{max})).

	Variable					
Species*	Intercept	Velocity ($m \cdot s^{-1}$)	Temperature (°C)	Fork length (mm)	Scale (σ)	Shape (δ)
American shad (702, 263,–569,gamma)						
β	5.706	–0.983	–0.029	0.0022	0.316	2.070
SE	0.291	0.032	0.010	0.0005	0.022	0.173
$P > \chi^2$	<0.001	<0.001	0.003	<0.001		
Alewife (222, 39, –319, gamma)						
β	4.571	–0.920	—	—	0.513	2.431
SE	0.169	0.074	—	—	0.075	0.412
$P > \chi^2$	<0.001	<0.001	<0.15	>0.15		
Blueback herring (81, 12, –94.9, Weibull)						
β	–0.435	–1.165	0.079	0.0196	0.665	
SE	1.991	0.149	0.029	0.0079	0.070	
$P > \chi^2$	0.827	<0.001	0.006	0.0131		
Striped bass (177, 36, –159, gamma)						
β	3.309	–0.854	0.024	0.0035	0.324	2.175
SE	0.440	0.050	0.015	0.0003	0.039	0.331
$P > \chi^2$	<0.001	<0.001	0.106	<0.001		
Walleye (49, 3, –15.3, Weibull)						
β	2.304	–0.679	0.039	0.0035	0.250	
SE	0.370	0.067	0.010	0.0009	0.031	
$P > \chi^2$	<0.001	<0.001	<0.001	<0.001		
White sucker (136, 24, –155, Weibull)						
β	4.399	–0.720	—	—	0.574	
SE	0.197	0.058	—	—	0.050	
$P > \chi^2$	<0.001	<0.001	>0.15	>0.15		

*Numbers in parentheses represent total N, censored N, log-likelihood, and distribution, respectively.

flume. Among those fish that did stage attempts, these models are conservative because they do not take into account the additional attempts that might have been staged had trial duration been extended for more than 1 h. In contrast, if fish that stage attempts quickly also swim farther (e.g., owing to superior condition or motivation), then the results shown here may be greater than expected for the population as a whole. This issue, as well as the effects of trial duration and attempt rate on estimates of swimming performance, is explored extensively elsewhere (Castro-Santos 2004).

Similarly, managers intending to apply these models should consider the potential effect of fatigue: the rate and distance of successive attempts may be affected by the extent to which fish exhaust their glycogen stores or other metabolic resources. Once depleted, these stores can take hours or even days to recover (Black et al. 1962) and, in some cases, can lead to postexercise mortality (Brobbel et al. 1996; Wilkie et al. 1997; Brick and Cech 2002).

This did not appear to be a concern here: fish showed no obvious signs of fatigue at the end of the trials, and no significant mortality occurred within 24 h after each trial. Moreover, biochemical analyses of blood and white muscle of American shad suggested that these fish did not swim to physiological exhaustion (Castro-Santos et al. 2000 and unpublished data). American shad did take longer to stage second attempts than their first attempt, and D_{max} tended to decrease with attempt number (Castro-Santos 2002). Later attempts occurred at greater rates, however, suggesting that the cause of the reduced distance may not have been physiological fatigue. By contrast, walleye and white sucker showed no evidence of reduced attempt rate on successive attempts (if anything, it increased), and distance of ascent was consistent across attempts (Castro-Santos 2004). Taken together, these data suggest that these species do not volitionally swim to physiological exhaustion when attempting to traverse velocity barriers.

The results of the regression models highlight some important differences among these species. Although all six species exhibited the expected decline in D_{max} with increasing velocity, variation among species in the magnitude of this effect differed from our expectations. For example, because American shad are by far the largest of the three alosine species, we expected the velocity effect to be smaller than among blueback herring and alewife. Instead, the effect was similar among the three species, with alewife showing the smallest and blueback herring the greatest response to increasing velocity. The contrast between blueback herring and alewife is interesting because of the morphological and ecological similarity of these two species. This difference occurred primarily because several alewife abandoned their efforts at short distances against the lowest velocity, resulting in a smaller overall velocity effect compared with the blueback herring. Despite this difference, blueback herring had greater overall D_{max} values, which is consistent with the fact that they often have greater migration distances and spawn in more lotic habitat (Loesch 1987).

Numerous studies have shown that temperature is positively correlated with endurance, especially at sustained

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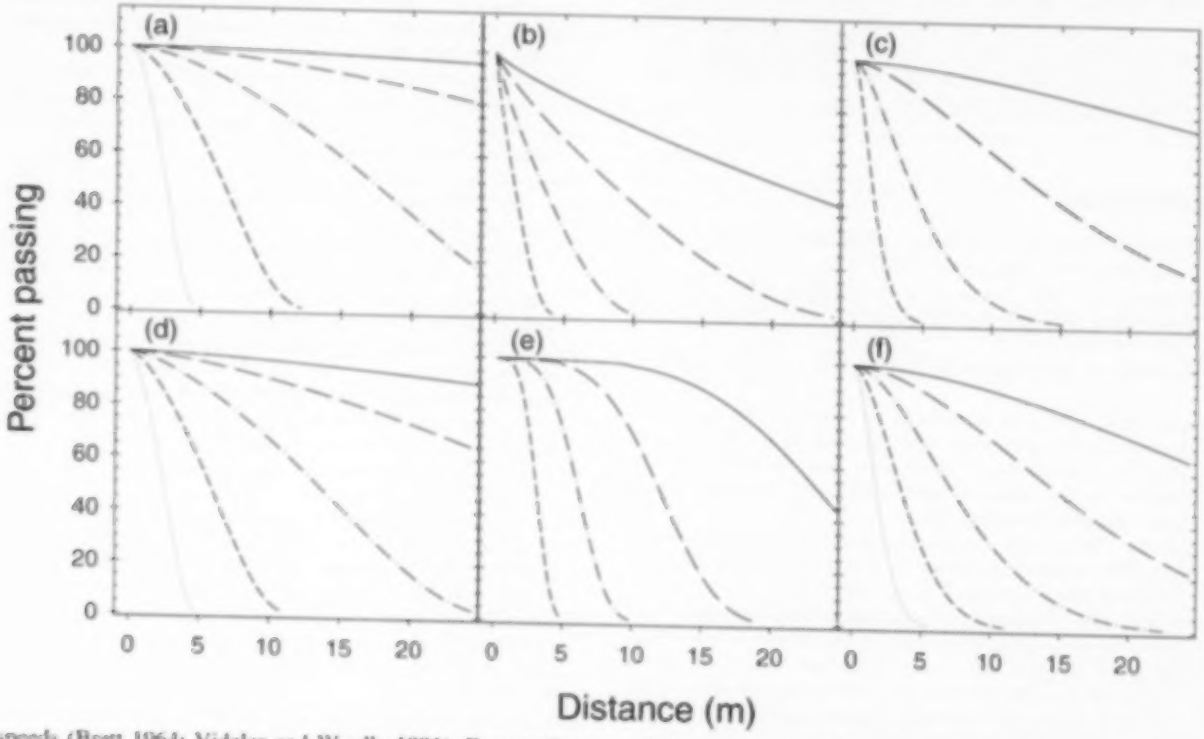
Fig. 5. Model predictions of percentages of (*a*) American shad, (*b*) alewife, (*c*) blueback herring, (*d*) striped bass, (*e*) walleye, and (*f*) white sucker successfully traversing velocity barriers. Velocities: solid line, 1 m·s^{-1}; long-dashed line, 2 m·s^{-1}; dashed-dotted line, 3 m·s^{-1}; short-dashed cline, 4 m·s^{-1}; dotted line, 5 m·s^{-1}. All other covariates are set to their mean values. To keep extrapolations on the same order as the interpolations, modeled velocities extend only to 4 m·s^{-1} for alewife, blueback herring, and walleye. Note that these predictions apply only to those fish that stage attempts within the first hour (see Castro-Santos (2002, 2004) for appropriate adjustments to account for attempt rates).



speeds (Brett 1964; Videler and Wardle 1991). Few studies quantify this effect on sprinting performance, however, and there is disagreement over its importance (Beamish 1978). We observed a positive correlation between temperature and D_{max} for blueback herring and walleye, but the opposite was true of American shad, and the effect among other species was not significant. Lack of significance should not be confused in this case with absence of effect: the range of temperatures at which species were run was variable and, because it corresponds to periods of fitness-crucial activity, may reflect a performance optimum for these species (Castro-Santos 2002). Thus, the signs of these coefficients may owe as much to nonlinear effects of migratory motivation as to physiological capacity. Also, because sprinting is largely powered by anaerobic processes, the temperature effects on sustained swimming may not be relevant. Temperature does not seem to be correlated with performance or recovery times during sprinting (Brett 1964; Schreer et al. 2001; Castro-Santos 2004).

As with temperature, many studies have shown length to be correlated with swimming performance, so much so that performance data are usually normalized for length, particularly when there is substantial variation in the lengths of the study animals (Bainbridge 1960; Brett 1965; Brett and Glass 1973). We, too, found significant correlations between length and D_{max}, but the effect was not universal and was much stronger among striped bass than among other species. Sexual dimorphism can obscure the effect of length on performance. In the case of American shad, females are larger than males, but much of their mass is devoted to eggs rather than to propulsive musculature. The small magnitude of the length effect in this species may be due to differences in performance between the sexes (see Castro-Santos (2002) for a detailed discussion of the effects of sex and length). The absence of a significant length effect among alewife and white sucker may be due to the relatively small variance in length for these species; similarly, and for the same reason, the strong length effect among blueback herring should be viewed with skepticism.

The information gained in this study defines performance of upstream migrant fishes swimming through velocity barriers in a novel way and at a realistic scale. The distance that fish are able to ascend high-velocity flow is a useful parameter for defining swimming performance and identifying potential distributional limits. Thus, the technical and numerical approaches that we have described have broad applicability both to site-specific fish passage problems and to understanding implications of velocity barriers for population ecology of migratory riverine species.

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Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers

Theodore Castro-Santos

Abstract: The ability of fish to migrate past velocity barriers results from both attempt rate and swimming capacity. Here, I formalize this relationship, providing equations for estimating the proportion of a population successfully passing a barrier over a range of distances and times. These equations take into account the cumulative effect of multiple attempts, the time required to stage those attempts, and both the distance traversed on each attempt and its variability. I apply these equations to models of white sucker (*Catostomus commersoni*) and walleye (*Stizostedion vitreum*) ascending a 23-m-long flume against flows ranging from 1.5 to 4.5 $m \cdot s^{-1}$. Attempt rate varied between species, attempts, and over time and was influenced by hydraulic variables (velocity of flow and discharge). Distance of ascent was primarily influenced by flow velocity. Although swimming capacity was similar, white sucker had greater attempt rates, and consequently better passage success, than walleye. Over short distances, models for both species predict greater passage success against higher velocities owing to the associated increased attempt rate. These results highlight the importance of attraction to fish passage and the need for further investigation into the hydraulic and other environmental conditions required to simultaneously optimize both attempt rate and passage success.

Résumé : La capacité des poissons de migrer à travers une barrière d'eau rapide résulte à la fois de la fréquence des tentatives et de la capacité de nage. Cette relation apparaît ici de façon formelle et des équations permettent d'estimer la proportion de la population qui réussit à traverser une barrière sur une gamme de distances et de temps. Ces équations tiennent compte de l'effet cumulatif de tentatives répétées, du temps requis pour organiser ces tentatives, ainsi que de la distance traversée à chaque tentative et sa variabilité. Les équations ont été appliquées à des modèles de meuniers noirs (*Catostomus commersoni*) et de dorés (*Stizostedion vitreum*) qui remontent une canalisation de 23 m contre des courants variant de 1,5 à 4,5 $m \cdot s^{-1}$. La fréquence des tentatives varie en fonction de l'espèce, et du temps, ainsi que d'une tentative à l'autre, et elle est influencée par les variables hydrauliques (vitesse du courant et débit). La distance de la remontée est surtout influencée par la vitesse du courant. Bien que la capacité de nage soit semblable chez les deux espèces, les meuniers noirs font plus de tentatives de remontée et leur taux de réussite est plus élevé que celui des dorés. Sur de courtes distances, les modèles des deux espèces prédisent un taux de réussite plus élevé dans les vitesses de courant plus fortes, parce qu'il y a, dans ces conditions, une fréquence plus grande de tentatives. Ces résultats mettent en lumière l'importance de l'attraction exercée par les passes migratoires et la nécessité d'études plus poussées sur les conditions environnementales et hydrauliques qui optimisent à la fois la fréquence des tentatives et la réussite des traversées.

[Traduit par la Rédaction]

Introduction

Studies on swimming performance of fishes are of intrinsic biological interest, and in the case of diadromous migrants, they also have an important applied component. The relevance of swimming performance to fish passage issues motivated some of the pioneering work of the last century in this field (Denil 1937; Bainbridge 1960; Brett 1962) and continues to receive attention today (Peake et al. 1997; Hinch and Bratty 2000; Haro et al. 2004).

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One factor that has limited the study of swimming capacity has been the challenge of observing fishes under controlled conditions that mimic their natural environments, making it difficult to formulate relevant hypotheses. For example, many carefully controlled studies have shown that critical swimming speed (U_{crit}) and other measures of performance increase with both temperature and length (Beamish 1978; Videler 1993). This has a broad physiological basis, yet may not accurately reflect the behavior of fish in the wild (Rome et al. 2000; Swank and Rome 2000). This is because volitional behavior is not governed exclusively by metabolism and biomechanics but, at least ideally, reflects a fitness-maximizing response to both environmental and endogenous cues. For example, the total discharge (Winstone et al. 1985; Aadland 1993; Holm et al. 2001) or chemical signatures issuing from a stream (Hasler 1971) may be as important a cue to the quality of upstream habitat as flow velocity or temperature. Given the appropriate stimulus, migrants of a range of sizes may be induced to swim upstream,

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even against currents or at temperatures that force them to swim at energetically costly prolonged or sprint speeds (Collins 1952; Weaver 1963; Webb 1975).

Another characteristic of laboratory studies that undermines their relevance to natural situations is the selective use of cooperative individuals (Brett 1964; Dewar and Graham 1994; Leonard et al. 1999). This practice tends to bias predictions of ability to traverse barriers (Castro-Santos and Haro 2003). Also, test fish are often of hatchery or cultured origin (Brett 1967; Peake et al. 1997) and are coerced into swimming, with either electric shock, prodding, confinement, or other external form of stimulation. Finally, laboratory studies typically attempt to generate a uniform flow profile, which reduces turbulence structure and low-velocity zones that fish might make use of in a natural setting. Although often necessary to obtain the desired data, each of these practices casts doubt on the accuracy of the predictions they are used to generate (Hammer 1995).

A similar criticism can be applied to the analysis presented in our companion paper (Haro et al. 2004) in which we analyzed data on swimming performance, quantified as the distance that fish were able to swim against a velocity challenge in an open channel. Fish were collected from a variety of sources and run over a range of dates and temperatures. We did this in part to guarantee a sampling of populations and conditions that represent the diversity of the region in which the tests were done. The resulting predictions of maximum distance of ascent (D_{max}), however, were based on the observed maxima of fish that entered during the first hour of each trial, ignoring the rate or frequency of attempt, the presence of individuals that staged no attempts, and the effects of successive attempts on ascent distance. Thus, effects of variability in motivation were largely excluded from our analyses. Here, I further develop the idea of swimming performance to include motivation, measured as attempt rate, and explore the implications of this variable on predictions of passage success.

Methods

A new model of swimming performance

Consider a scenario in which a group of fish with a common start time ($T_0 = 0$) is able to stage only one attempt to traverse a velocity barrier of distance D. The expected proportion of the population that will have passed by time T is equal to the proportion attempting multiplied by the proportion succeeding:

$$P(T,D) = A(T) \cdot S(D) \quad (1)$$

(see Table 1 for notation). The proportion blocked by the barrier equals the product of the proportion attempting and the proportion failing to pass:

$$B(T,D) = A(T) \cdot F(D) \quad (2)$$

The resulting functions increase with time as $A(T)$ approaches unity, but the proportion passing can never exceed $S(D)$.

A third population component comprises those fish that are available to pass but do not stage an attempt by time T.

$$N(T) = 1 - A(T) \quad (3)$$

Thus, the proportion of the population remaining below the obstacle consists of those that did not attempt to pass the obstacle as well as those that tried and failed to pass.

$$R(T,D) = N(T) + B(T,D) \quad (4)$$

When fish are allowed to stage successive attempts, however (as is generally the case), the probability of a given fish traversing a barrier becomes $1 - [F(D)]^n$, where n is the total number of attempts. As n increases, this value approaches unity for passable distances and zero for impassable distances (Fig. 1). In nature, the population of fish available to pass a barrier consists of individuals that have already staged one or more attempts and failed to pass as well as those that have yet to stage their first attempt. Of fish staging their first attempt before time T (or $t_1 < T$), the proportion that stages a second attempt will depend on the time t of their first attempt, i.e.,

$$A_2(T) = \int_{t=0}^{T} f_1(t)\, \hat{A}_2(T - t) \quad (5)$$

where t is time, incrementing by an arbitrarily small step Δt, $f_1(t)$ is the probability density function of attempt time, or the probability of staging a first attempt on the interval $(t - \Delta t, t)$, and $\hat{A}_2(T)$ is the cumulative distribution function of attempt time, conditional on fish having staged one attempt. Note that as the time of the first attempt approaches T, the probability of staging a second attempt goes to zero ($A(T)$ is, by definition, an increasing function with origin at zero and maximum of 1; Table 1). This logic can be extrapolated to successive attempts such that

$$A_a(T) = \int_{t=0}^{T} f_{a-1}^{*}(t)\, \hat{A}_2(T - t) \quad (6)$$

where a is the attempt number and $f_a^*(t)$ is the probability density function of attempt time, conditional on the probability density function of the previous attempt

$$f_a^*(t) = \int_{i=0}^{t} f_{a-1}^{*}(i) f_a(t - i) \,|\, a \geq 2 \quad (7)$$

$$f_1^*(t) = f_1(t)$$

Given information on timing and success rates of multiple attempts, eq. 6 can be combined with eqs. 2, 3, and 4 to predict the overall proportion of a population remaining below an obstacle. For example, allowing for two attempts:

$$R(T,D) = N_1(T) + N_2(T) \cdot B_1(T,D) + B_1(T,D) \cdot B_2(T,D) \quad (8)$$

The proportion remaining comprises those fish that staged no attempts, those that staged only one attempt and were blocked, and those that staged two attempts but were blocked on both. Note that, as with $A_a(T)$, $N_a(T)$ is the proportion failing to stage an attempt, conditional on having staged the previous attempt, and $B_a(T,D)$ is the conditional proportion that staged an attempt but failed to pass. Over k attempts, eq. 8 can be expressed as follows:

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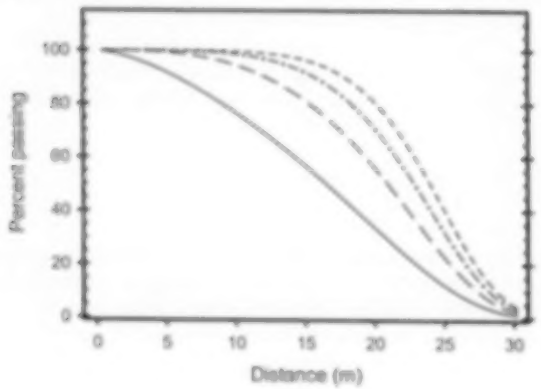
Table 1. Glossary of terms used throughout this paper.

Term	Meaning
D_{max}	Maximum distance of ascent within the flume (m)
U_t	Speed of flow (m·s^{-1})
Q	Volume of flow (i.e., discharge) (m^3·s^{-1})
$A_a(T)$	Cumulative distribution function of attempt a at time T, i.e., probability of staging an attempt at time $t \le T$. For $a > 1$, this function is conditional on having staged the previous attempt, and so $0 \le A_a(T) \le 1$
$N_a(T)$	Proportion of fish not staging attempt a by time T, i.e., the complement of $A_a(T)$
$f_a(t)$	Probability density function of attempt a at time t, i.e., unconditional probability of staging attempt a at time t
$F_a(D)$	Cumulative distribution function of attempt a at distance D, i.e., probability of failing at distance $d \le D$; $0 \le F_a(D) \le 1$
$S_a(D)$	Survivorship function of attempt a at distance D; equal to $1 - F_a(D)$ or the proportion successfully passing at distance D; $0 \le S_a(D) \le 1$
$B_a(T,D)$	Proportion of the population that attempts to pass the barrier but is unsuccessful on attempt a
$R(T,D)$	Proportion of the population that remains below the barrier because of either unsuccessful passage attempts or failure to stage attempts
$P(T,D)$	Joint probability of passage through distance D at time T

Fig. 1. Effect of multiple attempts on passage success. The prediction from the first attempt is for the expected distance of ascent by American shad (*Alosa sapidissima*) against 3 m·s^{-1} flow (Haro et al. 2004). The proportion of population passing increases exponentially with attempt number as $1 - [F(D)^a]$. Attempts (a): solid line, 1; long-dashed line, 2; dashed–dotted line, 3; short-dashed line, 4.



$$R(T,D) = \sum_{a=1}^{k}\left[N_a(T)\prod_{b=1}^{a}B_{b-1}(T,D)\right] + \prod_{a=1}^{k}B_a(T,D) \quad (9)$$

$$B_0(T,D) = 1$$

The complement of $R(T, D)$ is the cumulative proportion passing an obstacle.

$$P(T,D) = 1 - \sum_{a=1}^{k}\left[N_a(T)\prod_{b=1}^{a}B_{b-1}(T,D)\right] + \prod_{a=1}^{k}B_a(T,D) \quad (10)$$

This means that as the proportion of a population staging multiple attempts grows, the overall probability of passage also grows, even exceeding $S(D)$ (Fig. 1). Here, I demonstrate these methods using data from fish volitionally sprinting against controlled velocities in a large, open-channel flume.

Facilities, apparatus, and study animals

This study was conducted in the flume facility of the S.O. Conte Anadromous Fish Research Center (U.S. Geological Survey, Biological Resources Division) in Turners Falls, Massachusetts, located on the Connecticut River at river kilometre (rkm) 193. Details of the facility, the flume apparatus, hydraulics, and instrumentation as well as tagging, handling, and transport are described in Haro et al. (2004).

During the migratory seasons of 1997–1999, white sucker (*Catostomus commersoni*) and walleye (*Stizostedion vitreum*) were electrofished from the mainstem Connecticut River at rkm 278. Additional suckers were electrofished from the mainstem Connecticut River at rkm 183 and 98 or were collected from a fishway trap on the Westfield River (rkm 6, a tributary to the Connecticut with confluence at Connecticut River rkm 114). Fish were conveyed to the facility using a fish transport truck. There they were measured (fork length), sexed, externally tagged with uniquely coded passive integrated transponder (PIT) tags (Castro-Santos et al. 1996), held for 1–7 days in open, outdoor, flow-through holding ponds, and fed ad libitum pelletized feed (suckers) or shiners (walleye).

Before each trial, individual batches of fish were corralled (not handled) into the staging area below the swimming speed flume, where they were confined until the hydraulics were brought to the desired conditions (velocity, depth, etc.), usually for about 10 min. Trials lasted from 60 to 420 min and were assigned to a single nominal velocity condition of 1.5, 2.5, or 3.5 m·s^{-1}. White suckers were also subject to 4.5 m·s^{-1} (actual velocities varied; see Haro et al. (2004) and Table 2 for details). Because entry rates during the 1st hour were low for both species, trial duration was generally set to 360 min. During some trials, however, multiple species were present. In these cases, trials were of shorter duration, ranging from 60 to 180 min. This did not constitute a problem for these analyses, however, as will be shown below.

Velocity treatments were only semirandom, with greater emphasis placed on the 2.5 and 3.5 m·s^{-1} conditions, where large proportions of available fish entered the flume but failed to traverse its full length. Owing to the properties of flowing water and our desire to maintain uniform flow characteristics along the length of the flume, depths of flow dif-

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Table 2. Target and measured flow velocities (U_t, m·s^{-1}) and their SDs with associated discharge (Q, m^3·s^{-1}) (in parentheses). Also included are characteristics of white sucker and walleye trials, along with their SDs.

Nominal velocity	U_t (Q)	N	% attempting	Length (mm)	Temperature (°C)	Days held	Trial duration (h)
White sucker							
1.5	1.71 (1.64)±0.00	54	75.9	390±37	11.5±0.8	2.9±1.4	6.1±0.1
2.5	2.64 (0.69)±0.04	81	76.5	391±33	13.6±3.4	3.1±2.0	6.1±0.2
3.5	3.38 (1.52)±0.03	51	62.7	391±35	19.3±4.8	2.9±2.2	3.2±2.9
4.5	4.50 (2.07)±0.03	63	50.8	396±26	15.0±4.2	5.9±2.3	4.1±2.2
Walleye							
1.5	1.64 (1.57)±0.04	54	46.3	313±55	11.4±2.4	2.0±0.0	4.8±1.4
2.5	2.65 (0.69)±0.11	80	48.8	304±48	13.4±3.3	2.2±0.8	5.8±1.7
3.5	3.35 (1.51)±0.02	54	53.7	313±48	10.1±0.6	3.3±0.0	5.1±1.7

fered among velocity treatments. At 1.5 m·s^{-1}, the depth was 0.96 m; at 2.5 m·s^{-1}, it was 0.26 m; at 3.5 m·s^{-1}, it was 0.45 m; and at 4.5 m·s^{-1}, it was 0.46 m. Because the flume was 1.00 m wide and rectangular in cross section, the discharge (Q, cubic metres per second) was equal to the product of measured flow velocity U_t and flow depth. Also, because of the differing depths, the U_t:Q ratio varied by test condition, allowing for preliminary analysis of the separate effects of the two variables (Table 2).

Once the velocities had stabilized at the desired levels, an entrance gate was opened, the time was recorded, and fish were allowed to enter the flume of their own volition. Time of entry and maximum distance of ascent of each fish were logged using an array of PIT readers. These readers were spaced every 2.5 m from 0.5 m into the flume and interfaced with a central computer recording at 14 Hz. Although some fish were capable of exiting the top of the flume, the jet of water issuing from beneath the headgate (Haro et al. 2004) created a behavioral barrier through which most fish refused to pass; instead, fish that ascended to the top of the flume either lingered there or quickly fell back to the staging area.

At the end of each trial, the entrance gate was closed and fish were returned to the holding ponds. Tags were removed from the fish and they were returned to the river to continue their migrations. Thus, all fish used in this study were naïve, and cumulative effects from prolonged holding times were minimized.

Attempt rate

In part to maximize the number of fish and test conditions run, trials were terminated whether or not all individuals had staged attempts. This constitutes censoring with respect to time (Hosmer and Lemeshow 1999) and has important implications for the analysis of factors affecting attempt timing (Castro-Santos and Haro 2003). Regression models developed primarily for survival studies (accelerated failure time models: Allison 1995; Meeker and Escobar 1998) can be used to evaluate multiple covariate effects on data that include censored observations; I apply them here to quantify covariate effects on attempt timing.

For those fish that staged at least one attempt, the time elapsed between opening the gate and first detection by the PIT readers constituted the first attempt time: this is a complete (uncensored) observation. Those that never staged an attempt before the end of a trial (regardless of the duration of the trial) were included in the analysis, with attempt time set to trial duration, and designated as censored (incomplete) observations. In this way, all fish are included in the analyses, regardless of trial duration, and contribute to the estimates of $A(T)$ up until the time of censoring (Hosmer and Lemeshow 1999; Castro-Santos and Haro 2003). Similarly, subsequent attempt times were calculated as the time elapsed between their initiation and that of the previous attempt, i.e., the time between first detections of successive attempts. Censored observations were calculated as the time elapsed between the initiation of the previous attempt and the end of the trial. Thus, censoring times of the first attempts were mostly fixed at 6 h, but on subsequent attempts, censoring times were random.

The maximum read range of each reader was 0.5 m, so fish had to enter the flume to be detected. Individual attempts were defined as sequences of continuous records separated by no more than 30 s. This value was established empirically by reviewing preliminary data and was found to accurately describe the behavior of the fish: very rarely were fish present in the flume for more than 30 s without being logged by the nearest PIT reader. This method did, however, allow fish to probe the entrance of the flume multiple times before entering without generating a new attempt every time. This is a realistic criterion because fish swimming near the entrance may not be detected by the first reader for a short time but may still experience substantially greater velocities of flow (U_t) than in the rest of the staging area.

Because the intent of this paper is to illustrate the combined effects of attempt rate and maximum distance of ascent (D_{max}, metres), the regression models are as simple as possible, including only hydraulic variables (flow velocity (U_t, metres per second), discharge (Q, cubic metres per second), and $U_t(Q)$), temperature, length, and time elapsed between collections and trials (holding time) as candidate covariates. Discharge is included instead of depth in the analyses of hydraulic variables because it provides a more meaningful measure of the hydraulic characteristics of the staging area and therefore more accurately describes conditions that the fish were likely to perceive before entering the flume.

When fish staged multiple attempts, time (minutes) from the beginning of the trial to the beginning of each time interval (i.e., time to the previous attempt) was included as a covariate (start time). This allowed testing for correlations in

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attempt rate within individuals that were not adequately accounted for by other covariates. Such correlations can arise from informative censoring, which these statistical methods assume does not occur. Informative censoring means that censoring is not random with respect to the covariates, i.e., had censored observations been complete, they would not have had the same covariate response as the complete observations. The incomplete nature of censored observations means that there is no way to test for informative censoring statistically. However, inclusion of the time variable can help to offset any effect of informative censoring on the rest of the model (Allison 1995).

Methods of model selection and inference detailed in Burnham and Anderson (1998) were used to select the most parsimonious models from suites of models containing meaningful combinations of covariates. Thus, the $U_f Q$ interaction effect was only included in models that also included either or both of the main effects. Start times for attempts other than the first (i.e., time of the previous attempt) were included in all models, regardless of significance. Replicates of each model were constructed using lognormal, Weibull, and generalized gamma distributions (SAS Institute Inc. 1999; Meeker and Escobar 1998). Having generated the full series of models, the best one was selected using the adjusted Akaike's information criterion. This approach to model building has a strong foundation in information theory and avoids ambiguous and over- and under-fit models generated by stepwise methods (see Burnham and Anderson (1998) for an interesting review of this problem).

Distance of ascent

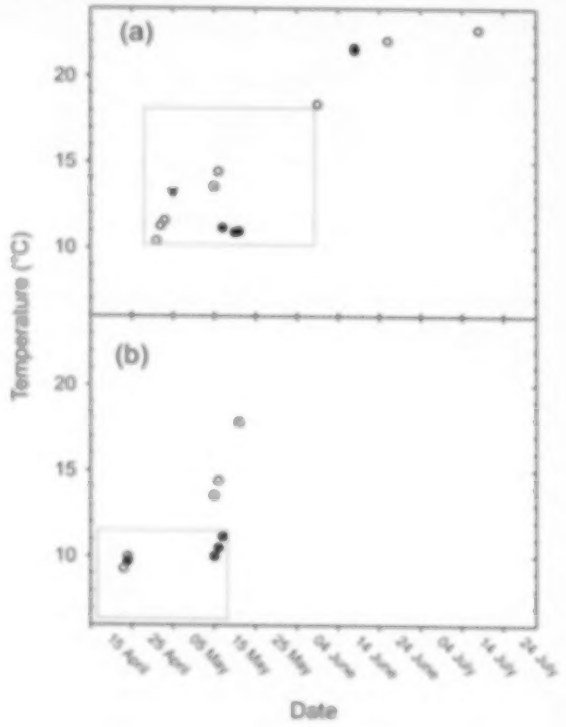
An analogous, but less conventional, approach to censoring is applied here in the analysis of swimming capacity, measured as the maximum distance (D_{max}) that fish swam once they entered the flume. The PIT readers used to log D_{max} were arrayed up to 18 m in 1997 and up to 23 m in 1998 and 1999. However, because fish may have been able to detect changing hydraulics and lighting at the head of the flume, all detections at or above 18 m were censored, regardless of year. Those that stopped before that distance were considered complete observations representing fatigue; censored observations indicate nonfatigue (throughout this paper, fatigue is defined by the decision to abandon an attempt, with no assumptions that fish are fatiguing in any physiological sense).

The same approach described above for attempt rate was used to develop models describing D_{max} for each attempt. Hydraulic variables pertaining to discharge were removed, and the time variable was removed from the repeat attempts, retaining only U_f, length, temperature, and holding time. Because it is unrealistic to expect U_f not to affect D_{max}, it was included in all models.

Combined effects of attempt rate and distance of ascent

After estimating attempt rates and distance of ascent for those fish that staged attempts, the combined effect of these functions was calculated using eqs. 6, 7, and 10 to generate an overall prediction of passage success at three velocities (2, 3, and 4 $m \cdot s^{-1}$) and at five evaluation times (30, 60, 120, 240, and 360 min).

Fig. 2. Dates and temperatures of trials of (*a*) white sucker and (*b*) walleye. Boxes indicate the expected range of spawning dates and temperatures.



Predictions of $A_s(T)$, $S_s(D)$, and $F_s(D)$ (Table 1) were generated using SAS software (SAS Institute Inc. 1999) for the first five (walleye) or six (sucker) attempts at each of these three velocities. Except for the hydraulic parameters (U_f, Q, and $U_f Q$), predictions were based on mean covariate values at each attempt. The cumulative effects were then calculated at each evaluation time and velocity to generate predicted passage curves based on both attempt rate and swimming capacity.

Results

In all, 249 suckers and 188 walleye were run during their respective migratory periods from 1997 to 1999 (Table 2). Sucker trials (N = 14) were conducted from April to July; walleye trials (N = 10) were run only during April and May (Fig. 2). For this reason, the sucker data cover a greater range of temperatures than the walleye data. Sucker trials comprised 18 ± 11 individuals (mean ± SD); walleye trials comprised 19 ± 3 individuals.

Attempt rate

The two species differed in attempt rate, with more suckers staging one or more attempts than walleye (Table 2). The percentage of suckers staging at least one attempt was similar at 1.5 and 2.5 $m \cdot s^{-1}$ but was less at 3.5 and 4.5 $m \cdot s^{-1}$. These data ignore differences in trial duration, however, and illustrate the importance of including a time axis. Under the 4.5 $m \cdot s^{-1}$ condition, the mean trial duration was 67% that of

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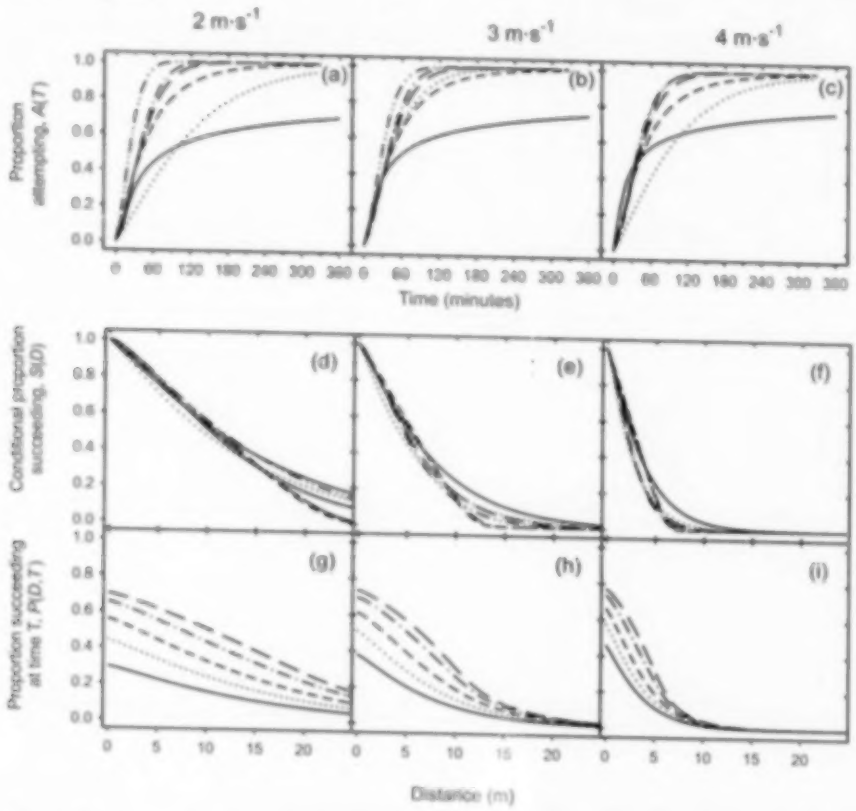
Fig. 3. Model predictions of attempt time (*a*–*c*), conditional success probability for the first six attempts (*d*–*f*), and combined probability of passage success over 6 h (*g*–*i*). Models are for white sucker ascending velocities of 2, 3, and 4 m·s^{-1} at 0.5 m depth. Predictions of *A*(*T*) and *S*(*D*) are for attempts 1 (solid line), 2 (dotted line), 3 (short-dashed line), 4 (dashed-dotted line), 5 (long-dashed line), and 6 (dashed–double-dotted line). Predictions of *P*(*T*,*D*) are for 30 (solid line), 60 (dotted line), 120 (short-dashed line), 240 (dashed–dotted line), and 360 min (long-dashed line).



the 1.5 and 2.5 m·s^{-1} conditions, so the observed difference was probably a function of trial duration (Table 2). Under the 3.5 m·s^{-1} condition, however, trial durations were even shorter, so the observed percentage of fish staging attempts may actually indicate a greater attempt rate under this condition. By comparison, the percent attempting and trial durations were more consistent among walleye trials, with the greatest attempt rate occurring under the 3.5 m·s^{-1} condition. Note that by quantifying attempt timing as *A*(*T*) (Figs. 3*a*–3*c* and 4*a*–4*c*), the inclusion of the time axis removes the ambiguities that arise from unequal trial durations (Kaplan and Meier 1958; Lee 1992). Moreover, the methods of survival analysis applied here permit the inclusion of multiple covariates that might also contribute to variations in attempt rate.

As mentioned in Haro et al. (2004), fluctuating headpond levels occasionally caused the hydraulic jump to move beyond 1.0 m into the flume. Attempts staged during these times were excluded from the analysis, as was the succeeding attempt (to avoid misleading values of elapsed time), although later attempts were included. Of the valid observations, numbers of suckers staging one to six attempts and of walleye staging one to five attempts (Event) as well as those available to stage events (total) are included in the regression models (Tables 3 and 4). These are accelerated failure time models and indicate covariate effects on the log of time (ln *t*, minutes)

Covariate effects on attempt times differed by attempt. Among white suckers (Table 3), hydraulic conditions affected attempt times on attempts 1, 2, 4, and 6. On the first attempt, discharge alone dominated attempt time, indicating that suckers took longest to stage their first attempt under the 2.5 m·s^{-1} condition (Table 2). On the second attempt, the model suggests similar attempt times under the 1.5 and 2.5 m·s^{-1} conditions, shorter attempt times under the 3.5 m·s^{-1} condition, but longer attempt times under the 4.5 m·s^{-1} condition. On the fourth attempt, attempt times increased with velocity. The effect of discharge on the sixth attempt was the converse of that on the first: fish entered most quickly under the 2.5 m·s^{-1} condition and most slowly under the 4.5 m·s^{-1} condition. Length of fish had no effect on attempt time, and temperature affected only the first (increased attempt rate) and sixth (reduced attempt rate) attempts. The temperature effect on the first attempt is important, as it suggests that initial attempt time decreased by a factor of $e^{(-0.108 \times 10)} = 0.44$ over 10 °C, allowing more time for subsequent attempts at higher temperatures. Duration of holding time also influenced attempt times of suckers, with increased holding times

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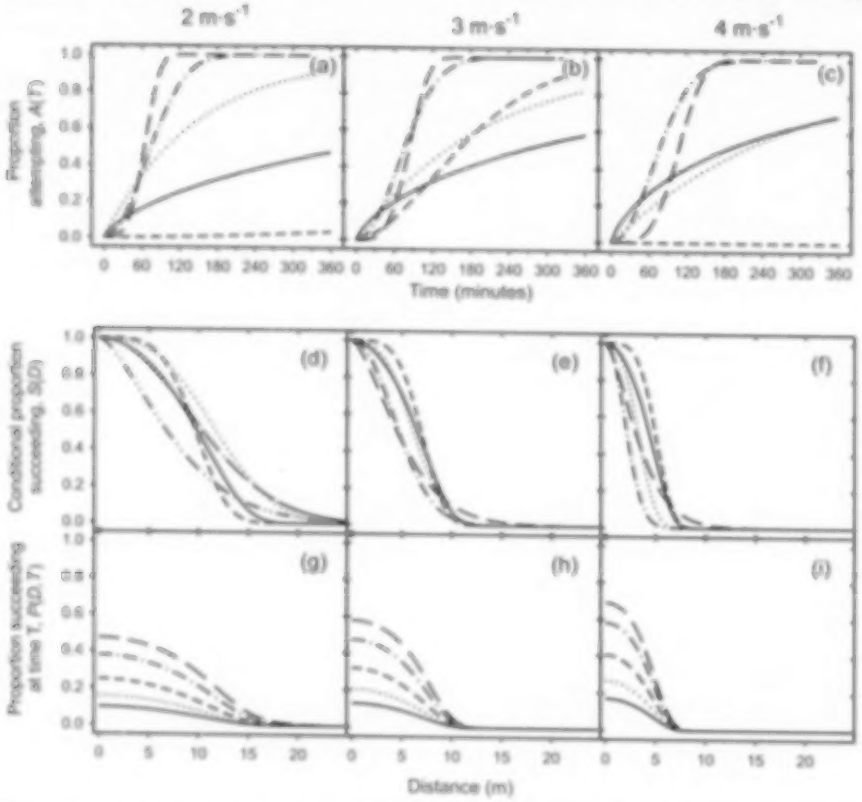
Fig. 4. Model predictions of attempt time (*a*–*c*), conditional success probability for the first five attempts (*d*–*f*), and combined probability of passage success over 6 h (*g*–*i*). Models are for walleye ascending velocities of 2, 3, and 4 m·s^{-1} at 0.5 m depth. Predictions of $A(T)$ and $S(D)$ are for attempts 1 (solid line), 2 (dotted line), 3 (short-dashed line), 4 (dashed–dotted line), and 5 (long-dashed line). Predictions of $P(T,D)$ are for 30 (solid line), 60 (dotted line), 120 (short-dashed line), 240 (dashed–dotted line), and 360 min (long-dashed line).



associated with reduced time to the first and sixth attempts: this means that attempt times of fish held for 7 days were reduced over those that were run on the first day by a factor of 0.52 on these two attempts.

Covariate effects on attempt time were also variable among walleye (Table 4). On attempts 1 and 3, the models indicate that hydraulic effects caused shortest attempt times under the 4.5 m·s^{-1} condition. The opposite effect is described for the second attempt, and on the fifth attempt, attempt time increased linearly with U_p. The length effect was significant only on the first attempt, with longer fish staging attempts more quickly than shorter ones. Similarly, shorter attempt times were associated with increased temperatures on this attempt. The effect here is much larger than for suckers, with time to the first attempt decreasing by a factor of 0.14 over 5 °C. As with suckers, attempt times were reduced with increasing holding times, affecting the first and third attempts. This indicates that walleye run on the first day after collection took more than six times longer to enter the flume the first time than those that were run on the fourth day (the maximum holding time for this species).

Suckers and walleye differed with respect to the effect of start time (time of attempt initiation) on subsequent attempt rates. This effect was at least marginally significant and consistent among suckers for attempts 2–6. A positive value here indicates that fish that took longer to stage a given attempt had lower rates of successive attempts as well. Specifically, if we assume a mean effect of 0.35, then fish that take 100 min to stage a given attempt will take $e^{0.35}$, or 1.4 times as long to stage their next attempt as fish that entered immediately. This heterogeneity of attempt rate suggests that there may be important covariates that were not included in these models. However, since the objective of this paper is to demonstrate the combined effects of attempt timing and swimming performance on D_{max} over time and not to test hypotheses or fully model the effects that dominate these factors, I will assume that inclusion of start time in the model adequately accounts for this unexplained variability.

Walleye, in contrast, showed no effect of start time on attempt rate except for on the second attempt, where significance was approached. This suggests that the rate of each attempt was effectively independent of the rate of the previous attempt, and no further modifications of the model are indicated. To be conservative, however, I include the start time variable in these models. Although this reduces the parsimony of the model, its inclusion had no substantial effect on the magnitude or significance of the other covariates.

Differences in attempt times of walleye and suckers are apparent in the amount of censoring present on each attempt.

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Table 3. Regression models of white sucker attempt times.

	β ± SE					
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5	Attempt 6
Intercept	5.51±0.37 ($P < 0.001$)	10.52±1.97 ($P < 0.001$)	3.67±0.16 ($P < 0.001$)	3.09±0.21 ($P < 0.001$)	3.62±0.20 ($P < 0.001$)	1.91±0.69 ($P = 0.006$)
U_t (m·s^{-1})	—	–2.48±0.71 ($P < 0.001$)	—	0.14±0.06 ($P = 0.026$)	—	—
Q (m^3·s^{-1})	–0.81±0.18 ($P < 0.001$)	–4.08±1.11 ($P < 0.001$)	—	—	—	0.49±0.16 ($P = 0.003$)
U_tQ (m^4·s^{-2})	—	1.47±0.39 ($P < 0.001$)	—	—	—	—
Length (cm)	—	—	—	—	—	—
Temperature (°C)	–0.08±0.02 ($P < 0.001$)	—	—	—	—	0.06±0.04 ($P = 0.086$)
Holding time (days)	–0.11±0.04 ($P = 0.007$)	—	—	—	—	–0.11±0.04 ($P = 0.005$)
Start time (min × 10^2)	—	0.42±0.14 ($P = 0.002$)	0.24±0.13 ($P = 0.069$)	0.39±0.10 ($P < 0.001$)	0.27±0.11 ($P = 0.015$)	0.49±0.13 ($P < 0.001$)
Scale	1.24±0.14	0.84±0.05	0.99±0.07	0.62±0.05	0.71±0.05	0.67±0.06
Shape	–2.33±0.44	—	0.63±0.18	—	—	—
Distribution	Gamma	Weibull	Gamma	Weibull	Weibull	Weibull
Total	249	166	148	128	112	104
Event	167	149	128	113	104	84
% censored	33	10	14	12	7	19

Note: Coefficients (β) and SEs indicate covariate effects on log attempt time (ln t, min). U_t, flow velocity; Q, discharge.

Table 4. Regression models of walleye attempt times.

	β ± SE				
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5
Intercept	15.74±1.75 ($P < 0.001$)	3.88±0.40 ($P < 0.001$)	36.60±10.67 ($P < 0.001$)	4.31±0.34 ($P < 0.001$)	3.71±0.45 ($P < 0.001$)
U_t (m·s^{-1})	—	—	–11.26±3.79 ($P = 0.003$)	—	0.25±0.13 ($P = 0.051$)
Q (m^3·s^{-1})	–0.83±0.40 ($P = 0.04$)	0.71±0.30 ($P = 0.019$)	–20.16±6.74 ($P = 0.003$)	—	—
U_tQ (m^4·s^{-2})	—	—	7.54±2.61 ($P = 0.004$)	—	—
Length (cm)	–0.07±0.03 ($P = 0.014$)	—	—	—	—
Temperature (°C)	–0.39±0.06 ($P < 0.001$)	—	—	—	—
Holding time (days)	–0.63±0.21 ($P = 0.003$)	—	–0.55±0.37 ($P = 0.135$)	—	—
Start time (min × 10^2)	—	0.39±0.21 ($P = 0.061$)	0.09±0.14 ($P = 0.490$)	0.19±0.18 ($P = 0.282$)	0.05±0.12 ($P = 0.650$)
Scale	1.36±0.12	1.01±0.10	0.58±0.069	0.48±0.07	0.26±0.05
Shape	—	—	—	—	—
Distribution	Weibull	Weibull	Weibull	Weibull	Weibull
Total	182	88	65	43	27
Event	88	61	42	27	15
% censored	52	31	35	37	44

Note: Coefficients (β) and SEs indicate covariate effects on log attempt time (ln t, min). U_t, flow velocity; Q, discharge.

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Because censoring was mostly fixed at 6 h on the first attempt, this can be viewed as an indicator of limits to the reliability of the models. Quantile estimates within this time frame are reasonable, especially for suckers, but the 52% censoring of walleye data on this attempt should alert readers to the need for caution in extrapolating far beyond estimates up to median attempt time. Censoring on subsequent attempts was random. The magnitude of censoring was small enough among sucker attempt models to discount any concerns that this may raise. Among walleye, however, censoring continued to be heavy on all attempts, and the results should be viewed with some skepticism, especially where significance is marginal (Allison 1995).

The Weibull and generalized gamma distributions provided a better fit to the data than did the lognormal distribution for all attempt time models. The scale (Weibull and gamma distributions) and shape (gamma distribution only) parameters indicate the shape of the underlying error distributions and hence of the cumulative attempt time functions ($A_x(T)$) for each attempt (Meeker and Escobar 1998; Haro et al. 2004). These are presented for suckers and walleye ascending under hypothetical hydraulic conditions of 2, 3, and 4 m·s^{-1} at 0.5 m depth and with other covariates set to their mean values (Figs. 3*a*–3*c* and 4*a*–4*c*, respectively). Note that predicted attempt times differ between species and among attempts.

Among suckers, the modeled rate of the first attempt is lower than subsequent attempts, which are then fairly consistent. On the first attempt, the rate is greatest under the 4 m·s^{-1} condition; on the second, it is greatest under the 3 m·s^{-1} condition. For both of these attempt models, the rate is least under the 2 m·s^{-1} condition. Attempt times are more consistent across velocities among the other attempt models, with $A(T)$ approaching unity within 3 h.

The attempt time models are much more variable among walleye. Here, strong but variable velocity effects predict greatest attempt rates under the 4 m·s^{-1} condition on the first attempt but lowest rates on the second attempt. On the third attempt, only the 3 m·s^{-1} condition predicts substantial proportions of fish attempting. The velocity effect on the fifth attempt was trivial by comparison with the first three.

Distance of ascent

Covariate effects on swimming capacity indicate that D_{max} was consistent among attempts by suckers, as was the effect of velocity (Table 5; Figs. 3*d*–3*f*). On the first attempt, D_{max} decreased by $e^{-0.70}$, or a factor of 0.50 for each metre per second increase in flow velocity. The coefficients for other attempts estimate the magnitude of this effect to range from 0.44 to 0.53 per metre per second increase. Length appeared to have no effect on D_{max}, and the only indication of a temperature effect was on the fourth attempt. On this attempt, D_{max} decreased by a factor of 0.67 over a 10 °C increase in temperature. Holding time appeared to have little effect on D_{max}, the only exception being on the second attempt, where fish held for 7 days swam only 67% as far as those run on the first day.

Model predictions for D_{max} of suckers swimming against hypothetical velocities of 2, 3, and 4 m·s^{-1} are presented for each attempt in Figs. 3*d*–3*f*. Proportion succeeding ($S(D)$) decreased almost linearly with distance down to the 50th

Table 5. Distance of ascent models of white sucker by attempt.

	β ± SE					
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5	Attempt 6
Intercept	4.10±0.25 ($P < 0.001$)	4.37±0.28 ($P < 0.001$)	4.17±0.13 ($P < 0.001$)	4.66±0.29 ($P < 0.001$)	4.35±0.27 ($P < 0.001$)	4.12±0.25 ($P < 0.001$)
U_f (m·s^{-1})	–0.70±0.08 ($P < 0.001$)	–0.78±0.11 ($P < 0.001$)	–0.65±0.05 ($P < 0.001$)	–0.64±0.07 ($P < 0.001$)	–0.82±0.09 ($P < 0.001$)	–0.76±0.08 ($P < 0.001$)
Length (cm)	—	—	—	—	—	—
Temperature (°C)	—	—	—	–0.04±0.02 ($P = 0.036$)	—	—
Holding time (days)	—	–0.07±0.04 ($P = 0.084$)	—	—	—	—
Scale	0.87±0.06	0.91±.07	0.35±0.05	0.37±0.09	0.76±0.07	0.71±0.08
Shape	—	—	2.77±0.45	2.91±0.72	—	—
Distribution	Weibull	Weibull	Gamma	Gamma	Weibull	Weibull
Total	167	149	128	113	104	84
Fatigued	148	132	112	94	89	72
% censored	11	11	13	17	14	14

Note: Coefficients (β) and SEs indicate covariate effects on the log distance of ascent (in D_{max}, m). Scale and shape parameters refer to disturbance terms of the accelerated failure time models of each distribution type. U_f, flow velocity.

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percentile with no noticeable difference among attempts and diverged only slightly thereafter.

Values for the walleye models were less consistent than those for the sucker models (Table 6). Coefficients for the intercept were uneven, and the velocity coefficient varied by a factor of 2.4. On the first three attempts, longer fish traversed greater distances, with no length effect thereafter. A significant temperature effect was present only on the third and fourth attempts. This effect differed in sign and was small on the third attempt (D_{max} decreased by 26% with a 5 °C increase in temperature) but more substantial on the fourth attempt (a 182% increase over the same temperature range). As with attempt time, walleye were more sensitive to holding time than suckers, except here, D_{max} decreased with increased holding time on attempts 1–3.

As with the attempt time models, the generalized gamma and Weibull distributions provided better fits to the data than the lognormal distribution. The finite length of the flume resulted in some censoring, particularly at low velocities. Overall, however, the proportion of censored observations was small (≤17% on all attempts), so these models can be considered reliable, at least up to 23 m, the length of the flume. The two notable exceptions are the fourth and fifth attempts by walleye, particularly the latter, where small sample size, not censoring, led to questionable estimates.

Model predictions of D_{max} for walleye swimming against hypothetical velocities of 2, 3, and 4 m·s^{-1} highlight the variability of capacity among attempts (Figs. 4*d*–4*f*). The shape of the survivorship curves ($S(D)$) took on more of a sigmoid shape than those of the suckers (Figs. 3*d*–3*f*). Despite these differences, the predicted D_{max} was similar between the two species at each of the velocities modeled.

To allow for comparison of effects of length, temperature, and holding time with the results presented by Haro et al. (2004), the above analyses were run on only the data of the 1st hour. The results differed from those found over the full 6 h. Among suckers, only length had a significant effect on attempt time (with time decreasing with increased length), and none of the three variables substantially influenced distance of ascent. Among walleye, the patterns were more similar to the 6-h data: the only effect of temperature was to increase attempt rate, and increased length was correlated with both increased attempt rates and increased distance of ascent. Holding time also affected performance of walleye, but in competing ways: attempt rate increased with increased holding time on the first three attempts, but distance of ascent decreased.

Also, to test for the possibility that the 1-h duration of the trials presented in Haro et al. (2004) selected for more motivated, and hence better-performing, individuals, I added attempt time to the first attempt D_{max} models (Tables 5 and 6). Time of entry was not correlated with D_{max} among suckers ($P = 0.776$). Among walleye, significance was approached ($P = 0.055$), but the effect was very weak ($\beta = -0.09$ per 100 min), suggesting that walleye entering after 100 min went 91% as far as those that entered immediately.

Combined effects of attempt rate and distance of ascent

The combined effects of attempt timing and swimming capacity are shown by the estimated overall proportion passing ($P(D, T)$, Figs. 3*g*–3*i* and 4*g*–4*i*). Here, separate curves

Table 6. Distance of ascent models of walleye by attempt.

	β ± SE				
Variable	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 5
Intercept	2.61±0.39 ($P < 0.001$)	3.43±0.56 ($P < 0.001$)	4.89±0.62 ($P < 0.001$)	2.36±0.82 ($P = 0.004$)	2.94±1.81 ($P = 0.104$)
U_i	–0.40±0.08 ($P < 0.001$)	–0.64±0.11 ($P < 0.001$)	–0.33±0.11 ($P = 0.002$)	–0.79±0.18 ($P < 0.001$)	–0.39±0.65 ($P = 0.546$)
Length (cm)	0.04±0.01 ($P < 0.001$)	0.03±0.01 ($P = 0.046$)	0.02±0.01 ($P = 0.030$)	—	—
Temperature (°C)	—	—	–0.06±0.02 ($P = 0.004$)	0.12±0.03 ($P < 0.001$)	—
Holding time (days)	–0.17±0.10 ($P = 0.091$)	–0.20±0.09 ($P = 0.037$)	–0.70±0.11 ($P < 0.001$)	—	—
Scale	0.28±0.05	0.35±0.04	0.23±0.03	0.49±0.09	0.68±0.16
Shape	1.86±0.46	—	—	—	—
Distribution	Gamma	Weibull	Weibull	Weibull	Weibull
Total	88	61	40	27	13
Fatigued	81	52	35	25	13
% censored	8	15	13	7	0

Note: Coefficients (β) and SEs indicate covariate effects on the log distance of ascent (ln D_{max}, m). Scale and shape parameters refer to disturbance terms of the accelerated failure time models of each distribution type. U_i, flow velocity.

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are drawn for predicted passage at five time intervals from 30 to 360 min. The importance of attraction is apparent: for both species, the greatest passage rates over short distances are predicted at each time step against 4 m·s^{-1} flow, succeeded with increasing distance by 3 m·s^{-1} flow. For both species, 2 m·s^{-1} flow yields the greatest passage success only over distances >4–6 m, even after 6 h. Just the opposite effect would be predicted from swimming capacity alone ($S(D)$, Figs. 3*d*–3*f* and 4*d*–4*f*). Indeed, at 6 h, the proportion of suckers expected to successfully pass the obstacle exceeds the maximum distance of ascent on any single attempt at distances >13 m, >5 m, and from 2.5 to 9 m (against 2, 3, and 4 m·s^{-1}, respectively). This is surprising, given that <80% of the fish are expected to even stage attempts under these conditions. Thus, the benefit of staging multiple attempts helped to mitigate for those fish that failed to stage any attempts.

Because of their lower entry and repeat rates, passage success of walleye did not accrue the same benefits as for suckers, rarely exceeding $S_a(D)$. This was particularly true under the 2 and 4 m·s^{-1} conditions, where very few walleye were predicted to stage more than two attempts. This is reflected in the censoring data as well (Tables 3 and 4): more than half of the available suckers staged at least three attempts, whereas only 23% of walleye did. Thus, hydraulic conditions clearly do limit passage success, with attraction serving a role fully as important as swimming performance in determining the outcome.

Discussion

This study quantifies the effects of both attempt rate and swimming capacity on passage success. This represents a departure from most current practices, which have focused exclusively on capacity (Bainbridge 1960; Peake et al. 1997, 2000). Recognizing the limitations of current practices, Bunt (2001) and Bunt et al. (1999), reported percentages of both attraction and capacity. This study differs from their approach, however, in three important ways: attraction is measured as a function of time, swimming performance is quantified as a function of ascent distance on successive attempts, and the combined effect of attraction and swimming capacity on overall passage success is explained. Elsewhere (Castro-Santos and Haro 2003), we have pointed out the limitations of recording event endpoints as percentages, when they in fact represent an instantaneous measure of a continuous, time-dependent process. This study further illustrates this point.

Effects of temperature, length, and holding time

Because the intent of this paper is to demonstrate the effects of repeat attempts on passage success, I have omitted many variables (e.g., sex, date, effort expended on previous attempts, recovery times, etc.) that might influence swimming performance and motivation. While trying to keep these models as parsimonious as possible, effects of temperature and length on swimming performance are so well established in the literature (Beamish 1978; Videler 1993) that I felt compelled to include them as potential covariates. Likewise, the potential effects of holding times on performance justified the inclusion of this effect. Comparison of the first hour's results here with those of Haro et al. (2004) helps to illustrate the interplay between attempt time and swimming capacity on passage success.

Among suckers, temperature, length, and holding time had little effect on attempt rate or distance of ascent during the first hour, consistent with the findings of Haro et al. (2004). Effects of these variables were present among walleye, however. Greater lengths were associated with both increased attempt rate and distance of ascent. Both of these factors should lead to increased D_{max}, which was the case (Haro et al. 2004). The only effect of temperature, however, was to increase the rate of the second attempt, with no affect on D_{max} on any single attempt. Still, D_{max} was positively correlated with temperature over this time period, suggesting that the increased attempt rate was responsible rather than any increase in capacity. Similarly, walleye that were held for longer periods had reduced D_{max} on each of the first three attempts. One might reasonably have expected this to produce a strong and significant effect on the combined data, but it did not. This follows directly from the increased attempt rate among walleye that were held for longer periods, counteracting the D_{max} effect.

Concerns raised by Haro et al. (2004) that our 1-h trials may have selected for more motivated, and therefore better-performing, individuals were not borne out in this study. Distance of ascent on the first attempt was similar among fish, whether they entered immediately or after several hours. No effect was present among suckers, and although significance was approached among walleye, the magnitude of the effect was trivial. Such an effect may have been present among the other species, but data were available for these tests only among suckers and walleye. It is interesting to note that although we ran all of our trials during the daytime, suckers and walleye typically migrate at night; it may be that the low rates of entry observed for these species had more to do with behavioral proclivities than physiological capacity. The relationship between motivation, behavior, and capacity is an interesting and potentially very important subject, one deserving of further study.

The results of this study also support the observations by Haro et al. (2004) and Castro-Santos et al. (2000) that these fish did not appear to be swimming to physiological exhaustion. Attempt rates increased after the initial attempt; just the opposite would be expected from fatigued fish. Similarly, the consistent D_{max} values among sucker suggests no cumulative effects from having staged previous attempts.

The inconsistent effects of length and temperature described in this study were surprising, given the wealth of data describing correlations between swimming performance and both of these variables. This is particularly true of the D_{max} models, where only the positive length effect among walleye matched expectations. Reproductive stage and status may explain the weakness of both effects. Females of both species are longer than males (Eschmeyer 1950; Quinn 1982): if males are more motivated swimmers than females, or if the egg burden limits swimming performance of females (Reidy et al. 2000), then this could confound the length effect among suckers. Among walleye, the largest individuals were excluded from our collections. Assuming that we had fewer females as a result (we were unable to consistently determine the sex of walleye), the presence of a length effect

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among walleye would be consistent with this pattern. Alternatively, anaerobic physiology may act to limit the performance benefits generally associated with large size. Goolish (1991) found that, owing to the scaling of power requirements and the allometry of anaerobic metabolism, burst-swimming capacity may actually decrease with size in some cases.

The only important effect of temperature for either species was to increase the rate at which fish staged their first attempts. This suggests some increase in motivation associated with greater temperatures. The effect was absent in later attempts, however. This is consistent with findings that suggest that the rate of recovery from anaerobic activity is largely independent of temperature (Brett 1964; Franklin et al. 1996; Schreer et al. 2001). Nevertheless, it is unclear why the increased motivation observed on the first attempt was not perpetuated in later attempts. Perhaps the initial delay reflected an ephemeral reluctance to enter an unfamiliar, high-velocity environment that was mitigated for by increasing temperatures. Once this reluctance was overcome, attempt rates increased, and temperature may have become unimportant.

The lack of a strong temperature effect on D_{max} (even negative in some cases) may reflect the presence of an underlying thermal optimum. Trials run later in the season (when temperatures were warmer) may have occurred near or past the end of the spawning period (Quinn 1982; Hamel et al. 1997), when motivation, and perhaps even swimming capacity, may have been declining.

Both of these factors underscore the importance of ecological and life history considerations when conducting performance studies. Studies should be done during periods and under conditions that are relevant to the animals in their native habitat, and temperature effects on metabolic processes and critical swim speeds (e.g., Brett and Glass 1973) may not be the most important determinants of swimming capacity, particularly at high speeds.

Hydraulic effects

Owing to the intrinsic properties of open-channel flow, we were unable to achieve the desired flow velocities using a constant depth of water in the flume. This means that flow velocity and discharge, while not perfectly orthogonal, were not directly correlated. Because both parameters can reasonably be expected to influence attempt rate (velocity because of its implications for performance and discharge because of its effects on the hydraulics of the staging area), both were included as potential factors in determining the adjusted Akaike's information criterion best model. The fact that each velocity was run at only one depth remains a weakness in our design, and the resulting predictions of hydraulic effects on attraction should be viewed as preliminary and subject to verification; further testing will be required to establish a rigorous relationship.

Within the confines of our design, the data do suggest separate but related roles of flow velocity and discharge. For both species, time to the first attempt was greatest under the 2.5 $m \cdot s^{-1}$ condition. Discharge was least under this condition, but it cannot be determined from our data whether the low attempt rates resulted from the low discharge or the shallow depth of flow (Haro et al. 2004).

Hydraulic effects were uneven in subsequent attempts, however. This was most noticeable among walleye, where a substantial proportion of the population was expected to stage a third attempt only under the 3 $m \cdot s^{-1}$ condition. Among suckers, the 3 $m \cdot s^{-1}$ condition was also most conducive to multiple attempts, owing to the greater rate of the second attempt. Variation in predicted attempt times as a result of the hydraulic conditions caused the models to predict superior passage through short distances against higher velocities, especially among walleye.

Readers should bear in mind that, although the models presented here have obvious potential for field applications, managers should use caution when interpreting these data. The hydraulic conditions in our flume mimicked only a small portion of the conditions that fish actually find in nature (Haro et al. 2004), and the staging area was entirely artificial. Thus, even where the D_{max} data may have broader applicability, the attempt rates observed here might not be representative of what one might expect to find in a field situation. Nevertheless, the effect of the various hydraulic conditions on attempt rate may serve as the basis for further study.

Effect of multiple attempts

The approach to calculation of D_{max} applied here differs from that used in Haro et al. (2004): here, I calculate separate models for each attempt, whereas in the previous paper, we calculated the overall D_{max} for each individual, regardless of how many attempts they staged. For this reason, readers comparing fig. 5 in Haro et al. (2004) and Figs. 3 and 4 here will note that on no single attempt do we expect fish to travel as far as they do when compared with the total data, even after only 1 h. This, in fact, is the premise for the model in eq. 10 and is the direct result of staging multiple attempts.

The methods used by Haro et al. (2004) do have some advantages, however. Their approach uses direct observation to estimate the likelihood of successful passage over a given distance by those fish that stage attempts. This requires fewer assumptions and many fewer parameters and modeling steps than the methods described here. As such, the models are likely to be more robust within the bounds of the modeled trial duration, but estimates of D_{max} will be conservative relative to what might be expected when these bounds are removed. Future studies that use trials of meaningful duration could use their method with minimal risk; but managers should bear in mind that the models may not realistically reflect changes in performance over time and, of course, must adjust for the proportion of the population that is expected to stage attempts.

The passage predictions ($P(D,T)$) presented here are superior to those of Haro et al. (2004) in that they expressly account for the proportion of fish that stage attempts as well as the number of attempts staged. To the extent that the staging area and flume entrance conditions differ from those found in natural or field environments, however, the broader applicability of these predictions is limited. Instead, these predictions should serve as an illustration of the importance of attraction and motivation to passage success, and the models should serve as templates for quantifying this effect in both field and laboratory situations.

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These methods are more likely to be useful where it is not feasible to run trials for extended periods or where delay is a concern. Using this approach, managers can estimate rates of successive attempts, even (modestly) extrapolating beyond the observed attempt number and trial duration. Because attraction is explicitly quantified as a time-based function, effects of varying rates of entry and reentry are readily incorporated into the models, and population-level effects of delay could be more accurately predicted. Also, because attraction and capacity are treated separately, identification of measures to improve either component is possible, and the effects of these improvements on passage performance can be estimated.

The results presented here demonstrate the importance of this approach over 6 h (the limits of our experimental protocol), but the technique has much broader application and relevance for field situations and for future studies where fish can be monitored for even longer periods of time. Such studies should select time periods that are appropriate for the population, species, and situation in question. Among fish with brief migratory periods or with strong diurnal constraints, 6 h may be an appropriate measure of acceptable delay. For fish that spend longer periods in fresh water, the period may be extended for days or weeks. Energetic constraints should also be considered: velocity barriers that require fish to swim in prolonged or sprint mode (powered by anaerobic metabolism) will be more costly than those that can be traversed in sustained mode (powered by aerobic metabolism; Webb 1975). The energetic costs of staging multiple attempts will therefore scale very differently depending on the swimming capacities of the individual fish. In each case, the expected costs and consequences of delay should be a factor in determining the biologically relevant scope of time allowed for fish to stage attempts through the velocity barrier.

In field applications, these methods must be modified to account for the fact that not all fish arrive at the staging area simultaneously. Thus, eqs. 6 and 7 can be generalized to all attempts, removing the restriction $a \geq 2$ and replacing the condition $f_1^*(i) = f_1(i)$ with $f_0^*(i) =$ the probability density function of the arrival times of fish to the staging area. If appropriate data are available, e.g., from radiotelemetry, fish that leave the staging area without passing can be included in the data set, with censoring time set to their time of departure.

The idea that fish are capable of staging multiple attempts, indeed required to do so in many instances, has been broadly overlooked in the fish passage literature (Farrell et al. 1998). Instead, predictions of passage success have focused on a deterministic view, derived from swimming speed – fatigue time models that identify theoretical maxima (e.g., Peake et al. 1997). These models ignore the fact of behavioral plasticity; the time at which fish abandon swimming efforts (generally assumed to indicate fatigue when the fish are coerced into swimming) is assumed to be a fixed function of swimming speed. This assumption is not always justified, and fish may elect to abandon attempts before fatiguing to maintain energy reserves for future attempts (Castro-Santos et al. 2000). Further, such models tacitly assume that fish swim at their optimal speeds and ignore the costs associated with deviating from these optima (Castro-Santos 2002).

These data demonstrate the importance of attempt rate and hence the importance of providing conditions that maximize attraction. Thus, passage must be thought of as a joint probability based on both attraction and capacity. Further, this probability will increase over time as fish stage multiple attempts. Conversely, fishways comprising multiple pools or chutes *require* fish to stage multiple attempts, and passage likelihood declines exponentially as $P(T,D)^w$, where w is the number of weirs, or steps, and consequently the minimum number of attempts required to pass.

Currents that challenge fishes' swimming capacity and those that fail to motivate passage attempts have important implications with regard to fitness and recruitment. Even subtle differences in the underlying performance structure of a population may affect passage success, ultimately leading to fragmentation of populations, with the associated loss of genetic diversity. Such loss is not necessarily harmful to populations: these are the very processes that lead to anadromous migrations in the first place, and the decision whether to expend energy on multiple efforts or to choose alternative spawning sites represents a trade-off that helps define a species' life history (Loesch 1987).

Still, fish passage structures that are constructed in such a way as to stimulate entry but that deny passage to large proportions of a population constitute artificial filters that have little relevance to the natural history and ecology of their target species. Passage may mimic natural selective processes but should do so in a way that is consistent with the stewardship objectives of conservation and mitigation.

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Reevaluating evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens

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Abstract: Analysis of length-at-age measurements of archived skeletal material shows that somatic growth rates of male northern fur seals (*Callorhinus ursinus*) vary inversely with population density. Von Bertalanffy growth curves were estimated for two series of known-age mandibles collected 1911–1920 (n = 156) and 1940–1953 (n = 151), time periods representing the historic population minimum and maximum, respectively. Mandibles from the former time period are larger than mandibles from the latter time period, suggesting a density-dependent response in somatic growth. Although density-dependent growth in northern fur seals has been suggested before, previous studies have been hampered by the potentially confounding factors of fisheries interactions, variable environmental conditions, and harvest of adult female northern fur seals. The material analyzed here pre-dates the substantial development of the Bering Sea groundfish fishery and the period of heaviest culling of females. Likewise, the two time periods examined are characterized by broadly similar climatic and environmental conditions. Therefore, the results support the hypothesis that measurements of somatic growth rates provide an index of population levels relative to carrying capacity. Growth rate studies could therefore be used to evaluate the current population status of northern fur seals.

Résumé : L'analyse des mesures de longueur en fonction de l'âge faites sur des os de l'otarie à fourrure du nord (*Callorhinus ursinus*) conservés en musée montre que la croissance somatique des mâles est inversement proportionnelle à la densité de la population. Nous avons estimé les courbes de croissance de von Bertalanffy pour deux séries de mandibules d'âge connu récoltées en 1911–1920 (n = 156) et en 1940–1953 (n = 151), des périodes qui correspondent respectivement au minimum et au maximum de densité de la population dans le passé connu. Les mandibules de la première période sont plus grandes que celles de la seconde, ce qui laisse croire à une réaction de dépendance de la densité dans la croissance somatique. Bien qu'on ait dans le passé indiqué que la croissance des otaries à fourrure est liée à la densité, les études antérieures sont embrouillées par la présence de facteurs confondants comme les interactions avec les pêches, les conditions variables de l'environnement et la récolte d'otaries à fourrure femelles. Le matériel que nous avons analysé a été récolté avant l'important développement des pêches commerciales des poissons de fond dans la mer de Béring et avant la période d'élimination maximale des femelles. De plus, chacune des périodes examinées se caractérise par des conditions climatiques et environnementales généralement similaires. Les résultats appuient donc l'hypothèse selon laquelle les mesures de croissance somatique fournissent un indice des densités de la population relativement au stock limite. Des études de taux de croissance pourraient servir à évaluer le statut actuel des populations d'otaries à fourrure du nord.

[Traduit par la Rédaction]

Introduction

Between the early 1950s and the 1970s, the population of northern fur seals (*Callorhinus ursinus*) in the Pribilof Islands, Alaska, declined approximately 60% (York and Kozloff 1987; York 1990; Sinclair et al. 1994). This decline is thought to have been caused primarily by direct take of adult females (York and Hartley 1981), a practice that was most prominent from 1958 to 1974. The Pribilof Islands population stabilized from 1981 to 1995 at a level considered to be "depleted" under the Marine Mammal Protection Act (United States Code 1972; Angliss and Lodge 2004) and has declined at a rate of 6% per year since 1998 (NMML 2004). Current management interests are aimed at understanding the various mechanisms that may have caused this stabilization and subsequent decline. One of the mechanisms that has received considerable attention is density-dependent regulation of vital rates such as mortality, survival, and growth

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(Fowler 1990). The research presented here expands on previous efforts to understand variability in somatic growth rate as a function of population level through the analysis of archived skeletal material collected 1911–1953 (for the use of other such indices see Swartzman and Haar 1983; Fowler and Siniff 1992). If the reaction of growth response of northern fur seals, hereinafter referred to as fur seals, to variability in population level can be accurately modeled, biologists will have a valuable tool for evaluating current population status and predicting future population trends (following the approach suggested by Fowler and Siniff 1992).

Somatic growth rates of fur seals have long been known to correlate inversely with population levels (Scheffer 1955), and this model has been refined through subsequent analyses (Baker and Fowler 1990; Fowler 1990; Trites and Bigg 1992). However, each of these studies utilizes different data (Table 1), making comparison of the results difficult. Furthermore, although variability in per capita food availability is clearly implicated, it is not clear if this correlation reflects changes in the abundance of prey items, the abundance of fur seals, or both (Trites and Bigg 1992).

The present study attempts to clarify the issue by utilizing measurements of archived skeletal material collected during two of the most noteworthy time periods of fur seal population history in the 20th century: 1911–1920, when the fur seal population was at its historic low of between 200 000 and 300 000 individuals, and 1940–1953, when the fur seal population had stabilized at its historic high of around 1.5 million (Lander 1980; York 1987). Hereinafter I will refer to these two time periods as popmin and popmax, respectively. Importantly, both of these time periods pre-date the development of extensive commercial fishing in the North Pacific Ocean/Bering Sea (Swartzman and Haar 1983; Trites and Bigg 1992, 1996). Thus, any variability in growth rates during these two time periods should be related primarily to variability in the abundance of fur seals rather than to fisheries-induced variability in the abundance of prey items (assuming no major oceanographic changes occurred over these time periods: see Discussion below). Furthermore, both popmin and popmax pre-date the period of extensive culling of adult females (1958–1974), which has been blamed for the population decline of the fur seal herd in the latter half of the 20th century (York and Hartley 1981). If variability in growth rates of fur seals is controlled primarily by population levels (coupled with feedback loops that "cascade" through the ecosystem; Estes 1996), then individuals collected during popmin are expected to grow faster and (or) to a larger overall size than individuals collected during popmax.

Numerous researchers have attempted to document density-dependent somatic growth in northern fur seals. In spite of the wide variety of data sets that have been employed, each of the studies detailed below has limitations related to sampling. Scheffer (1955) presented the first analysis of density-dependent growth in fur seals. The time periods represented in his study were 1913–1920 and 1941–1952, essentially the same as those covered by the present study. However, in his analysis Scheffer used mean measurements of length, weight, skull length, and skull width for discrete age classes (summarized in Table 1) and then compared means between time periods. This approach limited Scheffer to comparisons between four discrete age classes (3- to 6-year-old males) for the length and weight data, and only two age classes (5- and 6-year-old males) for the skull measurements. Nevertheless, Scheffer's data suggested that growth rates were lower during the population plateau (1941–1952) than during the population low (1913–1920).

Fowler's (1990) research on density-dependent growth in fur seals utilized a substantially different data set than Scheffer's to evaluate the same process. During the time period 1958–1974, 2050 males and 16 375 females were killed during pelagic research cruises for scientific study under the auspices of the North Pacific Fur Seal Commission (Lander 1980). Using data from these research cruises, Fowler (1990) regressed body size against pup production (as an index of population size) for 19 discrete age classes of females. Seventeen of those age classes showed significant negative correlation between body size and pup production.

Although it would seem that the question of whether or not fur seals display density-dependent growth has been abundantly supported in the affirmative, Trites and Bigg (1992, 1996) have challenged this interpretation on a number of grounds. The first is that studies based on the pelagic sampling of 1958–1974 mask significant seasonal fluctuations in measurements of body size (both mass and length) of adult female fur seals (Trites and Bigg 1992, 1996). When these seasonal fluctuations are taken into consideration, body size still shows a significant negative correlation with population level for the time period 1958–1974 (Trites and Bigg 1992). However, the latter years of this time period also coincide with unparalleled development of the commercial groundfish fishery in the eastern North Pacific and Bering Sea (Bakkala 1993). Trites and Bigg (1992) agree that the ultimate cause of variability in growth rates is related to per capita availability of food. But because the development of commercial fishing coincides with declines in the fur seal population, the effects of the two variables may be confounded for samples collected after the 1960s (Trites and Bigg 1992). Finally, Trites and Bigg (1992) point out that none of the previous studies effectively evaluates the role of climatic variability as regards per capita prey availability for fur seals.

Considering the merits and limitations of the previous studies, an approach that combines aspects of all of these previous studies is warranted. Because of the possible confounding factors of large-scale commercial fishing and the harvests of adult female fur seals, samples should pre-date the 1960s. Likewise, an index of body size is needed that has low measurement error and minimal seasonal fluctuation above and beyond the general trends in growth. Finally, an analytical approach that can utilize data from continuous, rather than discrete, age data will help account for variability in the season in which specimens were collected. Length-at-age data of archived skeletal material collected throughout the first half of the 20th century meet these criteria, and will be used to generate growth curves to evaluate if fur seals demonstrate density-dependent growth.

Materials and methods

This study utilizes measurements of the mandibles from skeletal specimens archived in the research collections at the

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Table 1. Data sets and time periods that have been the focus of previous attempts to document density-dependent growth in northern fur seals.

Study	Time period	Rationale	Measurement used	Age classes	Sample size
Scheffer 1955	1913–1920	Population low	Length	3- to 5-year-old males	214
			Weight	3- to 6-year-old males	248
			Skull length	5- and 6-year-old males	29
			Skull weight	5- and 6-year-old males	27
Scheffer 1955	1941–1952	Population high	Length	3- to 5-year-old males	4 753
			Weight	3- to 6-year-old males	211
			Skull length	5- and 6-year-old males	32
			Skull weight	5- and 6-year-old males	33
Fowler 1990	1958–1974	Population declining	Length vs. population	19 categories, females	16 375
			Length vs. population	2 categories, males	5 050
			Weight vs. population	19 categories, females	16 375
			Weight vs. population	2 categories, males	5 050
Baker and Fowler 1990	1948–1984	Population fluctuating	Tooth weight vs. population	3-year-old males	14 286
				4-year-old males	7 852
Trites and Bigg 1992	1958–1962	Equal time periods	Mass and length	1.5- to 4.5-year-old males	198
				1.5- to 4.5-year-old females	768
				5.5- to 15.5-year-old females	3 226
	1963–1968			1.5- to 4.5-year-old males	89
				1.5- to 4.5-year-old females	477
				5.5- to 15.5-year-old females	764
	1969–1974			1.5- to 4.5-year-old males	91
				1.5- to 4.5-year-old females	368
				5.5- to 15.5-year-old females	766
This study	1911–1920	Population low	Mandible length	0- to 8-year-old males	156
	1940–1953	Population high	Mandible length	0- to 11-year-old males	151

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National Museum of Natural History in Washington, D.C., and the National Marine Mammal Laboratory in Seattle, Wash. In most cases these specimens were collected specifically for age-determination studies (Osgood et al. 1915; Scheffer et al. 1984). For the time period 1911–1920 (popmin), 156 mandibles were collected representing cohorts born in 1908–1918 (Table 2). For the time period 1940–1953 (popmax), 151 mandibles were collected representing cohorts born in 1937–1953. These time periods are delineated primarily by the collection years of known-age specimens and by population trends (Osgood et al. 1915; Scheffer et al. 1984). The upper limit of the latter time period marks the beginning of the substantial harvesting of females — a practice that is blamed for the precipitous decline of the fur seal population in the late 1950s and early 1960s (York and Hartley 1981; Trites 1992*a*). As in all of the studies outlined above, this analysis will utilize cross-sectional rather than longitudinal data to estimate somatic growth rates.

The use of skeletal measurements has numerous advantages over approaches taken in previous studies. First, bone length is strongly correlated with body size (Scheffer 1950*b*; Scheffer and Wilke 1953). Consequently, bone measurements from known-age specimens provide an index of variability in somatic growth rate for each of the different time periods. Second, although the activity of osteoclasts and the rate of bone remodeling may vary by season, bone length is not expected to exhibit seasonal fluctuation to the same degree as body weight and body length (Trites and Bigg 1992, 1996), thus reducing the amount of background noise anticipated in the data set. A third advantage to using skeletal measurements is that such measurements are easily standardized, thereby minimizing measurement error. Fourth, the results of this study are easily replicable, with the possibility of verifying the age of any outliers by sectioning a canine tooth (Scheffer 1950*b*). Perhaps most importantly, the specimens utilized for this study were collected during the historic population low and high points. The data utilized here therefore hold the promise of showing the maximum expected differences in growth patterns of any time period in the 20th century. Furthermore, limiting my analysis to the time periods 1911–1920 and 1940–1955 eliminates two of the confounding factors identified by Trites and Bigg (1992) that have hampered other such studies: the substantial development of the pollock (*Theragra chalcogramma*) fishery and the harvest of adult female fur seals.

For the purposes of this study, age has been calculated in fractions of years. Although the annual average date of birth has been shown to vary between 3 and 11 July, depending on the year and analytical methods used (Trites 1992*b*; Gentry 1998), I have used Peterson's (1965) estimate of 7 July as the average day of birth to define zero age. I assume that the collection date is synonymous with the date of death of the individual. Given the remarkably synchronous birthing behavior of fur seals (75% of all births occur within a 3-week period; Trites 1992*b*), and the fact that the majority of the specimens studied here were collected specifically for age-determination studies, the calculated ages are not likely to be more than 1 or 2 months in error. However, a few individuals utilized in this study were aged via external examination of the upper canine (following Scheffer 1950*a*). This aging technique has a high degree of accuracy, with approximately 99% of age estimates falling within 1 year of the correct age (Anas 1970). Error rates in age determination are assumed to be similar for the two time periods considered here and should not bias the results significantly (Leberg et al. 1989).

Measurements were taken on the mandible of known-age male specimens. The specific measurement used here is termed mandibular short length (MSL) and is defined as the distance from the posterior margin of the last post-canine to the lateral margin of the mandibular condyle, measured on the lateral aspect of the mandible (Parkington 1972; Woodborne et al. 1995). MSL was measured to the nearest 0.01 mm on right mandibles when present, using digital calipers. In the absence of the right mandible, the left was used. A series of 361 paired mandibles was measured to evaluate any differences in MSL between sides. No significant difference between the two sides was found (paired $t = -0.124$, $p = 0.901$). Thus, the left mandible can be reliably used for this analysis in the absence of the right mandible.

The relationship between MSL and age was characterized by a von Bertalanffy (VB) growth curve (von Bertalanffy 1938, 1960) for each time period using nonlinear parameter estimation in SPSS (Norusis 1998). Although VB growth curves are most often found in the fisheries literature (Fabens 1965; Kimura 1980; Schnute 1981), their general applicability to length-at-age data makes them ideally suited for analyses of this type (McLaren 1993; Winship et al. 2001; but see also Day and Taylor 1997).

VB growth curves consist of a three- or sometimes four-parameter equation of the form

$$(1) \qquad Y(t) = y_{\infty}[1 - e^{-g(t-t_0)}]^p$$

where $Y(t)$ represents size at age t, y_{∞} is the asymptotic maximum size, g represents the rate at which size approaches the asymptote, t_0 is the age at which size is zero, and p describes the shape the curve takes as it approaches the asymptote.

One of the limitations of using the VB growth equation as formulated above is that it is often the case that nonlinear parameter estimation based on a minimization of the sums of squares fails to converge on an optimum solution (Schnute 1981). As a means of bypassing this problem, Schnute (1981) has developed a series of equivalent equations with parameters that have stable statistical estimates. Of the several equations presented by Schnute (1981), that which is most appropriate here is

$$(2) \qquad Y(t) = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}} \right]^{1/b}$$

Once again $Y(t)$ represents size at age t, but in this equation T_1 and T_2 are specified a priori and represent the youngest and oldest ages over which growth rates are to be calculated. Thus, four parameters remain to be estimated. Parameters a and b are equivalent to g and $1/p$, respectively, from eq. 1. That leaves y_1 and y_2, the estimated average size at ages T_1 and T_2, respectively. In addition to providing stable parameter estimates more reliably than eq. 1, eq. 2 eliminates the need to choose one of the several possible growth functions to describe a data set (Knight 1968; Ricker 1979; Schnute 1981). Furthermore, the parameters estimated for eq. 2 can

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Table 2. Age distribution of sample by cohort year.

	Age of specimen at time of collection (years)												
Cohort year	Pup	1	2	3	4	5	6	7	8	9	10	11	Cohort total
1908	—	—	—	2	—	—	1	—	—	—	—	—	3
1909	—	—	2	—	—	—	—	—	—	—	—	—	2
1910	—	—	—	—	7	—	—	—	—	—	—	—	7
1911	3	—	—	37	—	1	5	1	—	—	—	—	47
1912	—	—	14	8	20	6	3	29	6	—	—	—	86
1913	—	—	—	—	1	—	—	—	—	—	—	—	1
1914	2	—	—	—	—	—	—	—	—	—	—	—	2
1915	—	—	—	1	—	—	—	—	—	—	—	—	1
1916	1	4	1	—	—	—	—	—	—	—	—	—	6
1918	1	—	—	—	—	—	—	—	—	—	—	—	1
1937	—	—	—	1	—	—	—	—	—	—	—	—	1
1938	—	—	—	—	—	—	—	—	—	1	—	—	1
1939	—	—	—	—	—	—	—	—	1	—	—	—	1
1940	1	10	—	—	14	12	—	—	—	1	1	—	39
1941	2	1	—	24	2	2	21	6	4	—	2	1	65
1942	—	—	—	—	—	—	—	—	—	—	1	—	1
1943	—	—	—	1	—	—	—	—	—	—	—	—	1
1945	2	—	—	—	—	3	—	—	—	—	—	—	5
1946	—	—	—	1	4	—	—	—	—	—	—	—	5
1947	2	2	—	10	—	—	—	—	—	—	—	—	14
1948	—	—	9	—	—	1	—	—	—	—	—	—	10
1949	3	2	—	—	—	—	—	—	—	—	—	—	5
1950	—	1	—	—	—	—	—	—	—	—	—	—	1
1951	—	1	—	—	—	—	—	—	—	—	—	—	1
1953	1	—	—	—	—	—	—	—	—	—	—	—	1
Age class total	18	21	26	85	48	25	30	36	11	2	4	1	307

Note: The collection year can be determined by adding the age at time of collection to the cohort year (i.e., the 1908 cohortcollected as 3-year-olds was collected in 1911).

be used to calculate y_∞ and t_0 if they exist (which will not always be the case; see Schnute 1981).

The expectations of the hypothesis of density-dependent growth can be linked directly to the VB growth curve. As discussed above, individuals sampled during the historic population low (popmin) are expected to grow faster and (or) to a larger overall size than individuals from the historic population high (popmax). This can be evaluated in an approximate way by comparing individual parameter estimates (Kimura 1980) or by simultaneously comparing all of the parameters within the full VB growth curve model.

Results

Individuals available for this analysis ranged in age from pups to adults 11 years of age (Figs. 1 and 2;. Table 2). The age distribution of the samples has two important consequences for this analysis. The first is that although individuals at either extreme of the age distribution contribute to the overall solution of the parameter estimation, the growth curves for the two time periods are only comparable between 0.0 and 8.0 years of age (e.g., T_1 and T_2). While this age range encompasses most male fur seal growth, growth continues at a decreasing rate until the 10th year or so (Scheffer 1950*b*; Scheffer and Wilke 1953). Older individuals were collected during these time periods. However, external examination of the canines is not an effective way of estimating the age of animals older than 7–8 years (Scheffer 1950*a*). Consequently, they have been identified only as "adult" or " >10 years old", and have been omitted from this analysis. The second consequence of the age distribution is that because the samples do not cover the entire period of growth, no solution for asymptotic size (y_∞) exists for either cohort (Schnute 1981).

Keeping these limitations in mind, I plot MSL against age for each of the two time periods separately with the corresponding VB growth curves (Figs. 1 and 2). In spite of the fact that no solution for y_∞ can be calculated, the growth curves for the two time periods differ in the manner predicted under the hypothesis of density-dependent growth (Fig. 3): individuals sampled during popmin grew more quickly and (or) to an apparently larger size than during popmax. In point of fact, the two terms describing the shape of the growth curves (a and b) for each cohort are statistically indistinguishable (Table 3). Likewise, the estimates of y_1 (i.e., size at age $T_1 = 0.0$) are also statistically indistinguishable. However, the estimate of y_2 (i.e., size at age $T_2 = 8.0$) is significantly higher for popmin than for popmax (F ratio for equivalence of variance = 1.90, $p < 0.001$; Welch's $t = 3.75$, $p < 0.001$).

Before these results can be interpreted in terms of fur seal population levels, the available information on climatic variability in each of the two time periods needs to be evaluated, as advocated by Trites and Bigg (1992). As they point out,

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Fig. 1. Scatter plot of length-at-age data for mandibles from male northern fur seals (*Callorhinus ursinus*) collected between 1911 and 1920 (n = 156), with the corresponding von Bertalanffy growth curve.

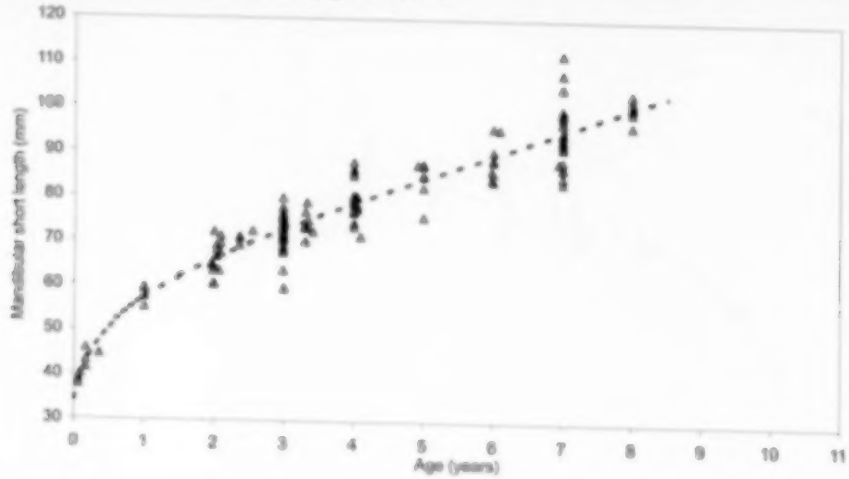
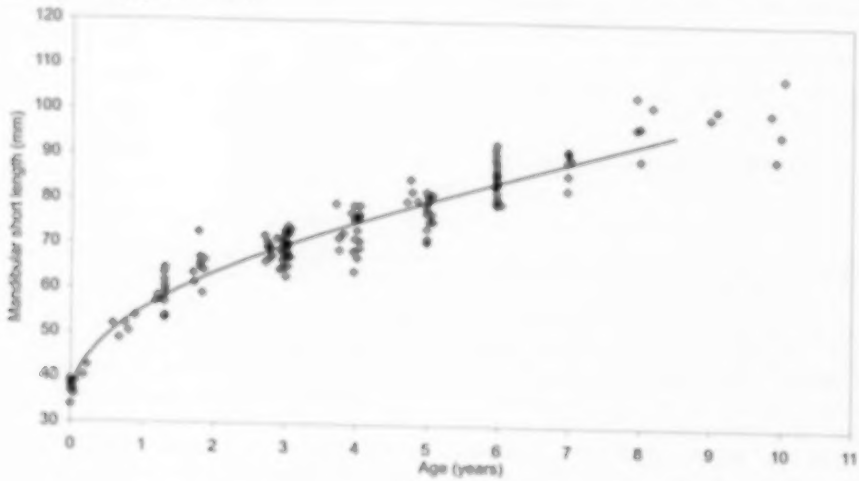


Fig. 2. Scatter plot of length-at-age data for mandibles from male northern fur seals collected between 1940 and 1953 (n = 151), with the corresponding von Bertalanffy growth curve.



there are numerous cyclic phenomena that act on interdecadal time scales that are likely to affect fur seal populations, prey availability, or both. In addition to the cycles specified by Trites and Bigg (1992) — 11-year cycle for sunspot activity (Waldmeier 1961) and 18.6-year cycle for lunar tidal node (Parker et al. 1995) — the Pacific Decadal Oscillation (PDO) might also be expected to affect prey availability in the North Pacific/Bering Sea (Ebbesmeyer et al. 1991; Francis and Hare 1994; Mantua et al. 1997). Finally, climatic forcing mechanisms that lack a clear cyclicity, such as the Aleutian Low pressure system, may also exert a direct influence on primary productivity in the North Pacific/Bering Sea (Trenberth and Hurrell 1994) and thus, indirectly, the availability of prey to fur seals.

Sunspot-activity cycles (Waldmeier 1961) appear to not play a role in this particular analysis, as both popmin and popmax span a complete cycle (Fig. 4*a*). The potential effects of variation in the lunar tidal node (Parker et al. 1995) are less clear; samples representing popmin were collected during a period of low tidal heights, while samples representing popmax were collected during a transition from high to low tidal heights (Fig. 4*b*). With regard to the PDO, Mantua et al. (1997) identify only one major regime shift in the 20th century, in 1977, with minor regime shifts possibly indicated in 1925 and 1947. However, based on their yearly average PDO index (a unitless measure defined as the principal component of North Pacific monthly sea surface temperature variability), both time periods sampled here experienced primarily negative index values (Fig. 4*c*).

Another valuable index of climatic variability in the North Pacific that spans the 20th century is Trenberth and Hurrell's (1994) North Pacific Index. The North Pacific Index is the area-weighted sea-level pressure over the North Pacific (30–65°N, 160–140°W) averaged over the months November–March. Periods of relatively low sea-level pressure correspond to intensification of the Aleutian Low pressure system. In-

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Fig. 3. Scatter plot of length-at-age data and the corresponding von Bertalanffy growth curves for male northern fur seals collected during popmin, 1911–1920 (- - △ - -) and popmax, 1940–1953 (—○—).

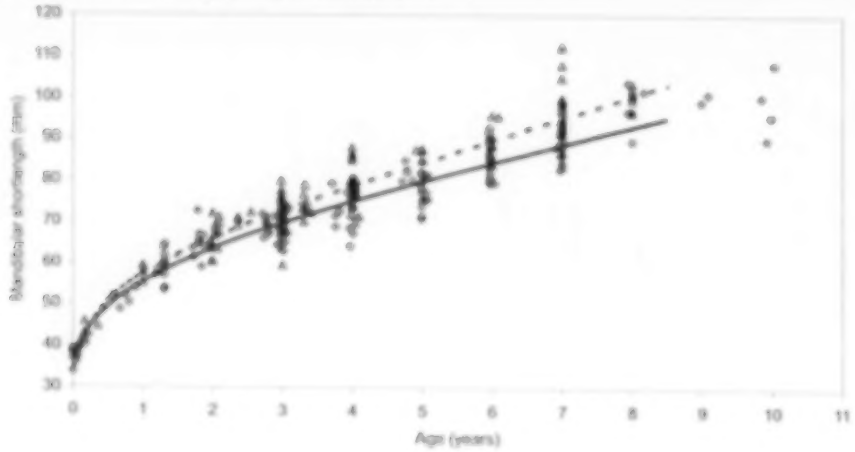

Table 3. Parameter estimates and summary statistics for von Bertalanffy growth curves generated using eq. 2 for popmin (1911–1920) and popmax (1940–1953).

	Parameter	Estimate	Asymptotic SE	Lower CI	Upper CI
Popmin (R^2 = 0.912, n = 156)	y_1	34.339	5.880	22.721	45.956
	y_2	100.610	0.982	98.670	102.551
	a	–0.283	0.122	–0.524	–0.041
	b	5.697	1.332	3.065	8.329
Popmax (R^2 = 0.935, n = 151)	y_1	36.682	1.401	33.914	39.450
	y_2	93.040	0.668	91.719	94.361
	a	–0.210	0.064	–0.336	–0.084
	b	5.472	0.751	3.988	6.956

Note: Starting values of 0.0 and 8.0 were used for T_1 and T_2, respectively. CI, 95% confidence limits.

tense Aleutian Lows are, in turn, associated with increased upwelling and marine productivity (Trenberth and Hurrell 1994). With the exception of the winters of 1941–1942 and 1945, both popmin and popmax occurred during periods of weak Aleutian Lows (Fig. 4*d*). Importantly, the popmax sample is dominated by the 1940 and 1941 cohorts sampled at a variety of ages (Table 2). Because the intensity of the Aleutian Low pressure system scales inversely with marine productivity, much of the popmax sample should have experienced enhanced prey availability.

In summary, then, it appears that animals collected during both popmin and popmax experienced broadly similar climatic conditions characterized by negative PDO index values and periods of weak Aleutian Low pressure systems. The exception to this generality is the winters of 1941–1942 and 1945, which were relatively intense winters associated with increased upwelling and marine productivity. In spite of the differences in these key years, animals collected during popmax were smaller than animals collected during popmin.

Discussion

The challenge to any evaluation of variability in growth rates of fur seals is to identify (*i*) the relevant mechanism(s) behind variability in prey abundance and (or) distribution and (*ii*) a climatic data series with sufficient scope of detail and coverage to make such an evaluation possible. Unfortunately, the specific effects that any given climatic perturbation may have on prey availability on either a local or a regional scale are largely conjectural, owing to a paucity of data from the early 20th century (Benson and Trites 2002; Sinclair and Stabeno 2002). Compounding this problem, fur seals travel thousands of miles annually along their migration route and consume over 60 different species of fish, squid, and krill (Kajimura 1984; Sinclair et al. 1994), whose overall contribution to the diet varies by region and year. The ability of fur seals to switch prey species, both temporally and spatially, has probably acted to buffer their populations to any but the most dramatic of shifts in oceanic productivity, making it difficult to predict whether shifts in productivity in the North Pacific, the eastern Bering Sea, or both would be significant. Furthermore, even if appropriate climatic data series were available, the mammalian communities of the North Pacific / eastern Bering Sea have undergone dramatic changes in abundance and composition over the past 200 years as a result of commercial harvests of pinnipeds (Busch 1985; Etnier 2002) and cetaceans (Trites et al. 1999; Springer et al. 2003), complicating analysis even further.

As the discussion above has made clear, there are a number of factors other than population level that could affect prey availability to fur seals and, by extension, the growth

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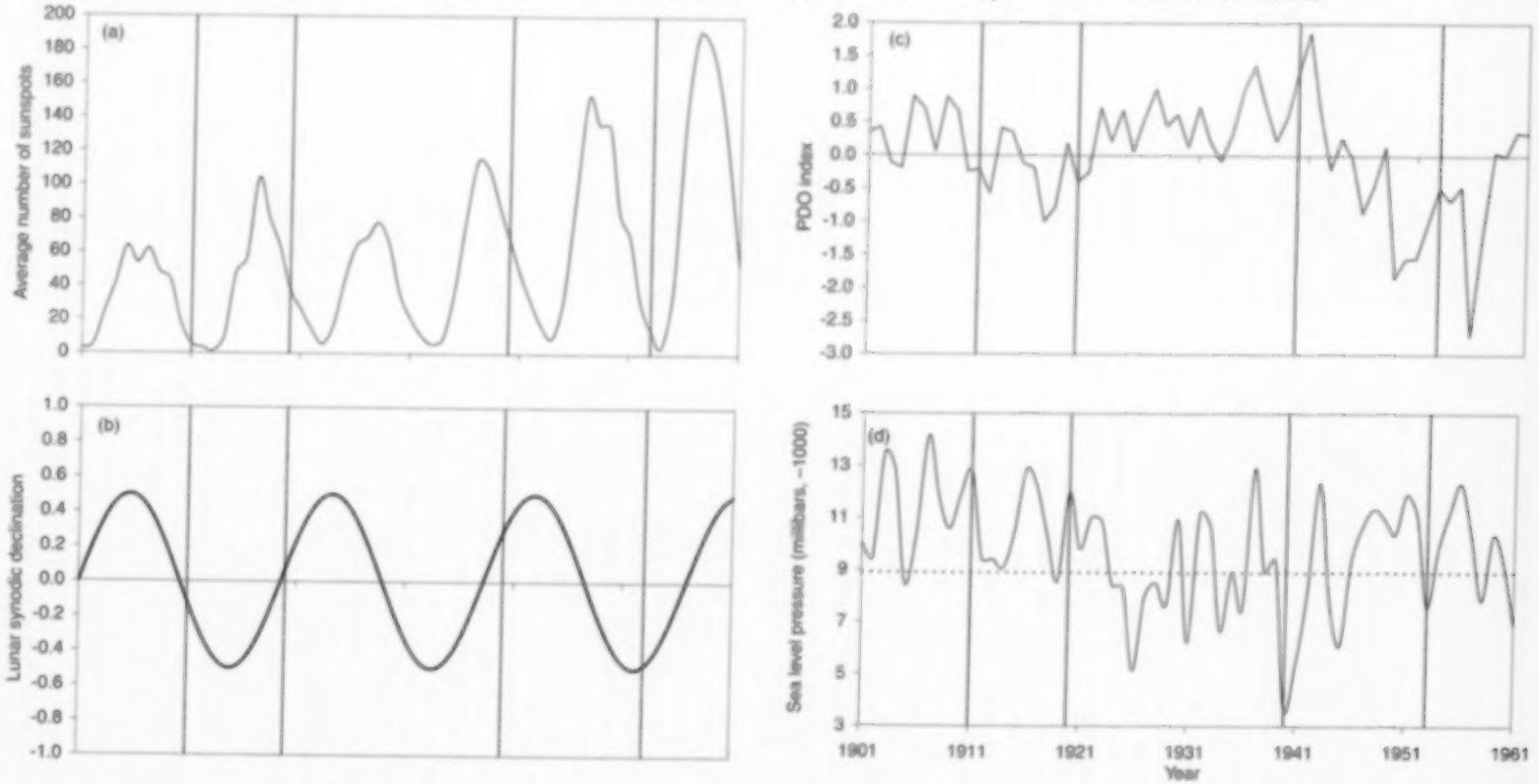
Fig. 4. Climatic events likely to affect prey availability for northern fur seals in the eastern North Pacific. Vertical lines bracket collection periods. (*a*) Average annual sunspot counts by year (Waldmeier 1961). (*b*) Lunar nodal tidal cycle by year (Parker et al. 1995). (*c*) Normalized mean winter (November–March) Pacific decadal oscillation (PDO) index values by year (Mantua et al. 1997). (*d*) Area-weighted mean winter (November–March) sea-level pressure in millibars (1 millibar = 100 kPa) over the region 30–65°N, 160°E–140°W (Trenberth and Hurrell 1994). The horizontal line is the average sea-level pressure over the time period 1925–1989 (1008.90 millibars).



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rates of fur seals. However, the fact that multiple studies have reached the same conclusion, that growth is density-dependent, based on dramatically different samples deriving from a wide range of temporal periods, suggests that the burden of proof should shift: have prey populations in the North Pacific / eastern Bering Sea fluctuated during the 20th century to the extent that fur seal populations have been significantly affected? Mass-balance models suggest that although the Bering Sea is relatively resistant to perturbations, reductions in prey abundance can quickly reduce marine mammal populations (Trites et al. 1999). Until this has been tested empirically (e.g., through stable-isotope analysis of archived skeletal materials; see Burton and Koch 1999), the evidence suggests, on balance, that fur seal growth rates are driven by fluctuations in population levels rather than by fluctuations in their prey base.

Although far from definitive, the results presented here provide additional support for the hypothesis that growth rates of northern fur seals are density-dependent. The failure to find a solution for y_∞ most likely relates to the sample of known-age individuals available from each time period. Nevertheless, the results indicate that individual fur seals grew to a larger overall size during popmin than during popmax: exactly the sort of difference expected under models of density-dependent growth.

This finding has significant implications for management of the current fur seal population. One of the possible explanations for the stabilization of the population at ~40% of the historic high is that there was a change in the carrying capacity (K) of the North Pacific / Bering Sea in the 1980s and 1990s (Sinclair et al. 1994). There is currently no explanation for the decline since 1998, but Fowler and Siniff (1992) suggested that pup survival rates in the 1980s might indicate a reduction of K by about 13%. Although a number of casual factors have been implicated, two of the most prominent are the major PDO of 1977 (Ebbesmeyer et al. 1991; Francis and Hare 1994; Mantua et al. 1997) and the continued development of the commercial groundfish industry (Trites and Bigg 1992; Bakkala 1993). The demonstration that fur seals are density-dependent in their growth rates provides a means to test this hypothesis. If the fur seal population has adjusted to a lower K, individual growth rates should be at a minimum. They should therefore be comparable to growth rates during the time period 1940–1955. In contrast, if the fur seal population is still well below K and something other than per capita prey availability is causing the population decline, growth rates should be at a maximum, comparable to growth rates during the time period 1910–1920.

Although adequate samples do not currently exist to test this hypothesis using VB growth curves based on mandibular measurements, the added support for the hypothesis that growth rates are density-dependent suggests that it may not matter what index of growth rate is measured. As long as comparable data (such as body size) can be generated for the time periods of interest, the current status of the fur seal population relative to K could, at least in theory, be evaluated (Fowler and Siniff 1992). Because a small-scale subsistence harvest of subadult male fur seals is still being conducted in the Pribilof Islands (Angliss and Lodge 2004), data of this nature should be easily obtainable.

In conclusion, the approach used here of analyzing archived skeletal material to evaluate density-dependent growth in fur seals has two distinct implications. The first, and most obvious, is that the results provide additional support for the hypothesis that individual growth rates of fur seals are density-dependent, and that variability in population levels can result in significant differences in growth rates. This does not deny the importance of other factors such as indirect competition with commercial fishing or climatic variability. Indeed, because the fur seal population is declining from an already depleted level (United States Code 1972; Angliss and Lodge 2004), an evaluation of the relative roles of commercial fishing and climate in maintaining the current population structure should now be possible.

The second implication of the results presented here is that it is possible to relate growth rates directly to population levels using measurements from skeletal material. This opens up the possibility of obtaining long-term data on relative population levels from palaeontological or archaeological samples. Because samples of this nature routinely span hundreds or thousands of years, the added time depth provided by these sources of data would make them a powerful tool for evaluating long-term trends in the population history of this species (Etnier 2002).

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The replacement of a native freshwater amphipod by an invader: roles for environmental degradation and intraguild predation

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Abstract: We assessed the extent to which an invader, *Gammarus pulex* (Crustacea: Amphipoda), has replaced a native, *Gammarus duebeni celticus*, over a 13-year period in a European river system and some of the abiotic and biotic factors that could account for this. Between 1988 and 2001, 56% of mixed-species sites had become invader-only sites, whereas no mixed sites had become native only again. The native dominated areas of higher dissolved oxygen and water quality, with the reciprocal true for the invader. Field transplant experiments revealed that native survivorship was lower in areas where it had been replaced than in areas where the invader does not yet occur. In invader-only areas, native survivorship was lower than that of the invader when kept separately and lowest when both species were kept together. We also observed predation of the native by the invader. Laboratory oxygen manipulation experiments revealed that at 30% saturation, the native's survivorship was two thirds that of the invader. We conclude that decreasing water quality favours replacement of the native by the invader.

Résumé : Nous avons déterminé dans quelle mesure l'espèce envahissante *Gammarus pulex* (Crustacea : Amphipoda) a remplacé l'espèce indigène *Gammarus duebeni celticus* sur une période de 13 ans dans un bassin versant d'Europe et étudié certains des facteurs abiotiques et biotiques qui pourraient être responsables de ce phénomène. Cinquante-six pour cent des sites qui contenaient les deux espèces en 1988 ne contenaient plus en 2001 que l'espèce envahissante, alors qu'aucun de ces sites ne contenait que l'espèce indigène. L'espèce indigène domine dans les zones de concentration d'oxygène plus élevée et de meilleure qualité de l'eau, alors que l'espèce envahissante prédomine dans les sites de concentration d'oxygène plus faible et de qualité de l'eau inférieure. Des expériences de transplantation sur le terrain montrent que la survie de l'espèce indigène est plus faible dans les sites d'où elle a été éliminée que dans les sites dans lesquels l'espèce envahissante n'est pas encore parvenue. Dans les zones où il n'y a que l'espèce envahissante, la survie de l'espèce indigène est plus basse que celle de l'espèce envahissante lorsque les deux sont gardées séparément et encore plus basse quand les deux espèces sont gardées ensemble. Nous avons aussi observé que l'espèce envahissante est un prédateur de l'espèce indigène. Des expériences de manipulation de l'oxygène en laboratoire montrent qu'à une saturation de 30 %, la survie de l'espèce indigène n'est que les deux tiers de celle de l'espèce envahissante. Nous concluons que la détérioration de la qualité de l'eau favorise le remplacement de l'espèce indigène par l'espèce envahissante.

[Traduit par la Rédaction]

Introduction

During biological invasions and range expansions, exclusions and replacements of native species by invading species are often caused by interspecific interactions (Diamond and Case 1986; Dick et al. 1993; MacNeil et al. 1999). However, successful invasions often accompany environmental degradation, thus questioning the role of biotic interactions (Conlan 1994; MacNeil et al. 2000*a*; 2001*a*). The rate of aquatic invasions may be increasing, with systems such as the North American Great Lakes poised for "invasional meltdown" (Ricciardi 2001), and research priorities now focus on the factors that facilitate invasions and the impact of invaders on native species (Ricciardi and Rasmussen 1998; Ricciardi 2001; Dick et al. 2002). Amphipod crustaceans have featured in many well-documented invasions throughout the world because of both coincidental transport with humans and deliberate introductions for fish farming, an-

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gling, and ecological experiments (Dick et al. 1997; MacNeil et al. 1999).

Since the mid-1950s in Northern Ireland, populations of the native freshwater amphipod *Gammarus duebeni celticus* have been subjected to invasion by *Gammarus pulex* transplanted from England (Strange and Glass 1979; MacNeil et al. 2001*a*). Consequently, there now exist pure and mixed assemblages of these species in numerous rivers and lakes (Dick 1996; MacNeil et al. 2001*a*). Hynes (1954, 1955) noted that *G. duebeni* is invariably eventually replaced by *G. pulex* when the two species meet and the invasion of Irish waters by *G. pulex* represents an ideal opportunity to assess the role of biotic interactions in coexistence and replacement. Indeed, laboratory studies have indicated that intraguild predation (IGP) (see Polis et al. 1989), principally the superior ability of *G. pulex* to resist predatory attacks and to prey on moulted *G. d. celticus*, is the major "driving force" behind the replacement of the native (Dick et al. 1993; Dick 1996; MacNeil et al. 1999). However, the role of abiotic factors in mediating such biotic interactions remains unexplored.

Although Hynes (1954, 1955) regarded *G. duebeni* and *G. pulex* as "ecological equivalents", being of similar size and using similar resources, Dennert (1974) noted that the outcomes of competitive interactions between the two species appeared to vary with the environment in which they took place, citing the higher tolerance of an extreme range of temperatures and salinities by *G. d. celticus* than by *G. pulex*. In addition, *G. pulex* has been unable to expand its range in areas of Brittany where *G. d. celticus* dominates (Stock 1993), and Dick et al. (1997) found that *G. d. celticus* had not been overwhelmed by introduced *G. pulex* in some rivers in the Isle of Man, concluding that environmental factors probably "alter the balance of interaction(s) between the species". Both Holland (1976) and Meijering (1991) inferred from field data that low oxygen represented a major factor determining the distribution of several riverine *Gammarus* spp., with the latter author finding that *G. pulex* occupied those rivers with the lowest oxygen levels, where other *Gammarus* spp. were absent. Indeed, in a survey of several Northern Ireland rivers invaded by *G. pulex*, MacNeil et al. (2001*a*) found that sites with only *G. d. celticus* or co-occurring with *G. pulex* had higher dissolved oxygen levels and higher biological water quality than sites where only *G. pulex* occurred. However, no experiments have been carried out to assess if *G. d. celticus* can survive the physicochemical regimes of sites where they have been replaced by *G. pulex*. In addition, no field experiments have been attempted to assess IGP between the native and invader under physicochemical regimes where both currently co-occur, and no experiments have been attempted to assess differential tolerances of the native and invader to dissolved oxygen level.

The present study aimed to (*i*) assess range expansion of *G. pulex* in the River Lagan, Northern Ireland (Strange and Glass 1979), where *G. pulex* incursions were first recorded in detail 13 years ago (see Dick et al. 1993); (*ii*) assess if abiotic factors, particularly dissolved oxygen and water quality, correlate with differences in the current distribution of the two species in the Lagan system; (*iii*) use field transplant experiments to assess if *G. d. celticus* can survive the physicochemical regimes of areas of the Lagan where *G. pulex* has replaced the native; (*iv*) assess the role of IGP under such field conditions; (*v*) assess differential tolerances of the two species to dissolved oxygen level; and (*vi*) assess if differences in oxygen level could influence survivorships of the two species when they co-occur.

Materials and methods

Field survey

The location and details of the study area in Northern Ireland are shown in Fig. 1. The extent of the replacement of *G. d. celticus* by *G. pulex* during the past 13 years was investigated by sampling at 26 sites along the River Lagan and several of its tributaries that were originally sampled in 1988–1989 (see Dick et al. 1993). Sites were sampled during April–May 2001 (spring–summer) and again during the period November 2001 – January 2002 (autumn–winter).

At each site, initially starting from the mid-channel riffle section and gradually moving to the river margin and bank, three replicate 3-min kick samples (0.9-mm-mesh net) were taken. All macroinvertebrates were preserved on site in 70% ethanol. *Gammarus* were counted and identified to species and other macroinvertebrates to family level. Biological water quality was assessed by the average score per taxon (ASPT) biotic index (Armitage et al. 1983). ASPTs were generated for each site (three kicks combined) with the Gammaridae removed from the calculations to negate their influence on the values (MacNeil et al. 2001*a*).

Prior to kick-sampling, in situ values for "site-level" environmental variables were obtained: water temperature (mercury thermometer), pH (Gallen Kampf meter), dissolved oxygen (Jenway DO_2 meter 9071), conductivity (Dist WP, Hanna Instruments), percent tree and riffle coverage (both estimated visually), water depth and current velocity (C2 OTT flowmeter), and wet width of the river channel (MacNeil et al. 2001*a*). Five-day biochemical oxygen demand (BOD_5) was obtained for each site using standard laboratory methods (Sykes et al. 1999). With each kick sample, we determined the percent macrophyte and leaf litter coverage (visually estimated) and substrate characteristics (minimum, maximum, modal, and mean dominant particle sizes, all via phi scale, substrate heterogeneity by number of discrete substratum types present). "Catchment-level" variables including the site's altitude and channel slope were also obtained (see MacNeil et al. 2001*a*). The above environmental variables were selected because all may influence the distribution of *Gammarus* spp. (Holland 1976; MacNeil et al. 2000*b*, 2001*b*). Data were transformed as necessary to normalize their distribution prior to analysis (Appendix A).

Environmental data (Appendix A, 19 variables) were analyzed by principal components analysis (PCA) to characterize environmental gradients of the river sites (MacNeil et al. 2001*a*). PCA was performed separately for spring–summer and autumn–winter samples to avoid the predominance of seasonal effects over spatial differences (Feijoó et al. 1999). PCA was then used to generate component scores that reflect the contribution of each component to each site.

Correlations between individual environmental variables and environmental gradients as defined by component scores and (*i*) percent *G. pulex* of total amphipods (arcsine transformed) and (*ii*) the sensitivity/tolerance of the wider macro-

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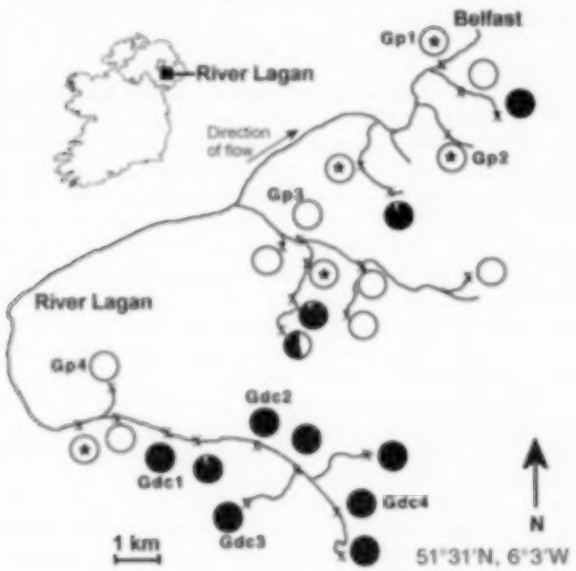

Fig. 1. River Lagan survey sites in Northern Ireland (inset) showing 2001–2002 distributions and relative abundances of *G. d. celticus* (solid circles) and *G. pulex* (open circles). Only 25 sites are shown and not the original 26 because one was lost due to dredging. Xs indicate the exact places of sampling. The asterisks indicate *G. pulex* only sites in 2001–2002, which were mixed-species sites in the 1988–1989 survey (note that Gp2 had 3% native individuals in spring–summer but 0% in autumn–winter). Bioassay transplant tube sites are designated Gdc1–Gdc4 (*G. d. celticus*) and Gp1–Gp4 (*G. pulex*).

invertebrate assemblage (as estimated by ASPT) in each site allowed assessment of how environmental factors influenced the distribution and relative abundance of *G. pulex* and *G. d. celticus*. Generation of large numbers of correlation coefficients carries the risk that a number may be significant by chance; nevertheless, we present *p* values for inspection by the reader.

Field transplant experiment

In May 2001, eight study sites were selected in the River Lagan, four sites where *G. d. celticus* occurred alone (Gdc1–Gdc4) and four where *G. pulex* occurred alone (Gp1–Gp4) (Fig. 1). *Gammarus d. celticus* and *G. pulex* were collected by kick-sampling from mixed-species sites (UK grid references J306646 and J269589) but housed separately overnight in large plastic trays with a plentiful supply of source water and substrate/leaf material. Mortality was zero during this period. Collecting from mixed-species sites meant that individuals of both species would be equally favoured or disadvantaged by being moved to single-species sites. Only healthy, acanthocephalan parasite free, nongravid adult *G. pulex* (approximately 10–14 mm body length) and *G. d. celticus* (12–16.5 mm body length) were chosen for experiments. Bioassay tubes were plastic pipe (length 20 cm, diameter 5 cm) covered at both ends with nylon mesh of 1-mm pore size (one end with a screw cap). This mesh size was a compromise between being large enough to allow the free flow of water and to prevent clogging with silt/debris and being small enough to retain amphipods (Turnbull and Bevan 1995; MacNeil et al. 2000*a*). Each tube was secured to a slate base by a pipe clip and supplied with 10 individual amphipods (see below), stream-conditioned English oak (*Quercus robur*) and European black alder (*Alnus glutinosa*) leaves from the site, five catfish food pellets (each 0.5 cm in diameter), and substrate in the form of two 5-cm strands of Canadian pondweed (*Elodea canadensis*) and five hollow stone tubes (each 1 cm in diameter). The range and quantity of food items chosen were designed to cover the omnivorous nature of the amphipod diet (see Kelly et al. 2002).

At each of the four *G. d. celticus* only sites, six tubes, each containing 10 *G. d. celticus*, were placed. No tubes containing *G. pulex* were placed at these native-only sites because of ethical considerations about possible escapes. At each of the four *G. pulex* only sites, 18 tubes, six containing 10 *G. d. celticus* only, six containing 10 *G. pulex* only, and six containing five *G. d. celticus* with five *G. pulex*, were placed. Unfortunately, bioassay tubes could not be deployed in mixed-species sites because pilot studies revealed that they were frequently disturbed by people (C. MacNeil, personal observation). Tubes were orientated 45° to the water flow, allowing free flow through the tube with minimal deposition of sediment and preventing amphipods from being forced to one end of the tube (Turnbull and Bevan 1995). Tubes were randomly placed throughout each site, and in *G. pulex* only sites, each *G. d. celticus* tube was tied to both a *G. pulex* tube and a mixed-species tube such that both single- and mixed-species assemblages were exposed to similar microhabitats and hydrological regimes. In this way, individual tubes of each species were used as the replicate sample unit (see Gibbins et al. 1994; MacNeil et al. 2000*a*).

Tubes were examined weekly, dead amphipods removed, additional food supplied, and tubes placed back on the substrate. At the same time, physicochemical measurements (pH, conductivity, current velocity, and dissolved oxygen) were taken at each site. Survivorships (proportion of the initial numbers arcsine transformed) of *G. d. celticus* in single-species tubes in *G. d. celticus* only and *G. pulex* only sites were compared in a two-factor analysis of variance (ANOVA), the factors being "site" and "time" (repeated measure). Survivorships of *G. d. celticus* and *G. pulex* in single-species tubes in *G. pulex* only sites were compared in a separate two-factor ANOVA, the factors being "site" and "time" (repeated measure). Survivorships in mixed-species tubes were compared in a three-factor ANOVA, the factors being "species" (repeated measure), "site", and "time" (repeated measure). Differences in physicochemistry between *G. d. celticus* and *G. pulex* sites were examined using separate two-factor ANOVAs, the factors being "site" (either *G. d. celticus* or *G. pulex*) and "time" (repeated measure). The statistical package SuperANOVA (Anonymous 1989) was used.

Laboratory experiments

During June 2001, *G. d. celticus* and *G. pulex* were collected from *G. d. celticus* dominated and *G. pulex* only sites, respectively (grid references J269589 and J335685, respectively). The two species were separated in the laboratory and then maintained for 2 weeks in tanks of water comprising

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25% from each source water and 50% dechlorinated piped water and substrate/leaf material with a 10 h light – 14 h dark cycle at 12 °C. Mortality was zero for both species during this period.

Short-term oxygen tolerance experiment (single species)

At 12 °C, three 10-L tanks containing filtered Lagan water had dissolved oxygen levels lowered to 20%, 30%, and 40%, respectively (Jenway meter 9071), by bubbling with nitrogen (approximately 5–20 min) (see Dick et al. 1998). Apart from the lowest oxygen level, these approximated those that both species could be exposed to in nature (MacNeil et al. 2000*a*; C. MacNeil, personal observation). For each of the three oxygen levels (20%, 30%, and 40%), 18 plastic pots, each of 385 mL volume, were filled to the brim with tank water and 10 adult *G. d. celticus* added to each of six pots, 10 *G. pulex* to each of six pots, and no amphipods in the remaining six pots (no food or substrate added). Size ranges for adult *G. d. celticus* and *G. pulex* were similar to those for the transplant experiment, but this time, individuals of the two species were matched for body size by eye (Dick et al. 2002). All pots were then sealed with transparent airtight lids. Although these amphipod densities were high, they did reflect similarly high densities that *G. pulex* in particular can reach in Northern Irish river systems (MacNeil et al. 2000*b*, 2003). Visual inspection at 7 and 24 h recorded the number of surviving amphipods in each pot. In empty pots, final oxygen levels were recorded at the end of 24 h to assess changes in oxygen concentration during the course of the experiment. Survivorships of *G. d. celticus* and *G. pulex* at different oxygen levels were compared in a three-factor ANOVA, the factors being "species", "oxygen level", and "time" (the latter as a repeated measure).

Longer term oxygen tolerance experiment (single and mixed species)

A 20-L clear glass tank containing filtered Lagan water (constituents as previously) had twenty-four 385-mL pots (eight pots each containing 10 adult *G. d. celticus*, eight pots each containing 10 adult *G. pulex*, and eight pots each containing five *G. d. celticus* with five *G. pulex*) placed at random on its bottom. Each pot was attached to the tank bottom by blu-tac. A substrate of clear glass beads (three 1.5-cm-diameter beads) and leaf food (one 3 cm × 2 cm section of conditioned alder leaf) was placed in each pot. Each pot was covered with 0.9-mm transparent plastic mesh, which pilot studies revealed prevented amphipods escaping from the pot while still allowing water to circulate between the pot and the rest of the tank. The 20-L tank was then filled to the brim with water. Oxygen levels in the tank were then lowered to 40% at 12 °C by bubbling nitrogen (approximately 1 h) through the water (see Dick et al. 1998). This oxygen level represented a low level for *G. d. celticus* (the lowest level in *G. d. celticus* only sites being 75%) but was found in mixed sites and was common for *G. pulex* only sites and was the lowest saturation that could be maintained at a constant level for several days. Pilot studies also revealed that identical oxygen levels in individual pots and the rest of the tank were achievable by this method. The tank was sealed airtight with a glass lid fixed on with parafilm. Daily visual inspection for 9 days recorded the number of surviving amphipods in each pot. After 9 days, oxygen levels were checked in the tank and random pots. The protocol was then repeated for new amphipod specimens but with an oxygen level of 85% saturation at 12 °C achieved by bubbling air through the water (approximately 1 h) (see Dick et al. 1998). Survivorships of *G. d. celticus* and *G. pulex* were analyzed separately in two three-factor ANOVAs, the factors being "oxygen", "treatment" (single or mixed species), and 'time' (the latter as a repeated measure).

Results

Field survey

One site contained neither species (owing to dredging) and thus was excluded from all subsequent analysis. Of the remaining 25 sites sampled, eight contained only the native, four contained both, and 13 contained only the invader (Fig. 1). These designations held true between seasons, except for Gp2, which had 3% natives in spring–summer and 0% in autumn–winter and thus was designated a *G. pulex* only site overall. Fifty-six percent of the mixed-species sites in 1988–1989 had become *G. pulex* only sites by 2001–2002, with the remainder still mixed. No mixed sites had become *G. d. celticus* only sites. *Gammarus d. celticus* and *G. pulex* only sites in 1988–1989 remained the same 13 years later.

During spring–summer, percent *G. pulex* was positively correlated with site width and BOD_5 ($r = 0.45$ and 0.47, respectively, both df = 23, $p < 0.05$) and negatively with riffle coverage and dissolved oxygen level ($r = 0.40$ and 0.51, respectively, both df = 23, $p < 0.05$ and $p < 0.01$, respectively). Percent *G. pulex* was also negatively correlated with ASPT, with pollution-tolerant macroinvertebrate families becoming more dominant as percent *G. pulex* increased ($r = -0.42$, df = 23, $p < 0.05$), and ASPT itself was negatively correlated with BOD_5 ($r = -0.49$, df = 23, $p < 0.05$). In autumn–winter, percent *G. pulex* was positively correlated with modal dominant particle size (i.e., smaller substrates) and BOD_5 ($r = 0.46$ and 0.44, respectively, both df = 23, both $p < 0.05$) and negatively with dissolved oxygen level ($r = -0.56$, df = 23, $p < 0.01$). There was a strong trend for percent *G. pulex* to again be negatively correlated with ASPT ($r = -0.39$, df = 23, $p = 0.06$).

From PCA, the first three component axes (PC1, PC2, and PC3) accounted for 66% and 61% of the variance for spring–summer and autumn–winter samples, respectively (see Table 1). For spring–summer, PC1 (32.6%) distinguished higher altitude, shallower sites with higher dissolved oxygen levels and dominated by larger substrates (i.e., cobbles/boulders) from lower altitude, deeper sites with lower oxygen levels and dominated by smaller substrates (i.e., sand, mud, gravel). PC2 (20.7%) distinguished sites with larger substrates from those with smaller substrates. PC3 (13.1%) distinguished slower flowing sites with smaller substrates from faster flowing sites with larger substrates. For autumn–winter, PC1 (30.1%) distinguished more upland, narrower river sites with a complex substrate matrix dominated by larger substrates from more lowland, wider sites with a less diverse substrate matrix dominated by smaller substrates. PC2 (19.3%) distinguished deeper sites with denser tree canopy cover and more leaf litter on the riverbed from those shallower sites with less dense tree cover and leaf litter. PC3

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Table 1. Loadings of the first three PC axes for spring–summer and autumn–winter with the 19 variables from which they were derived.

Variable[a]	Spring–summer			Autumn–winter		
	PC1	PC2	PC3	PC1	PC2	PC3
Slope						
Altitude	0.69			0.60		
Wet width				–0.61		
Depth	–0.79				0.66	
Current velocity						0.71
% riffle			–0.70			0.68
Substratum heterogeneity				0.76		
Mean substratum particle size		–0.77				
Minimum dominant particle size	–0.68					
Maximum dominant particle size		–0.87				
Modal dominant particle size			0.67	–0.79		
Dissolved oxygen	0.88					
BOD_5						–0.88
Conductivity		–0.65				–0.62
pH						
Water temperature						
Tree canopy cover					0.61	
Macrophyte cover						
Litter cover					0.60	
Eigenvalue	6.45	3.91	2.36	5.68	3.0	2.0
% variance explained	32.6	20.7	13.1	30.1	19.3	11.6

Note: Only the highest loadings (>0.6) for each variable are shown for the sake of clarity.
[a]Units for all variables are as in Appendix A.

(11.6%) distinguished faster flowing, riffle-dominated sites with lower BOD_5 and conductivity levels from slower, more pooled sites with higher BOD_5 and conductivity levels.

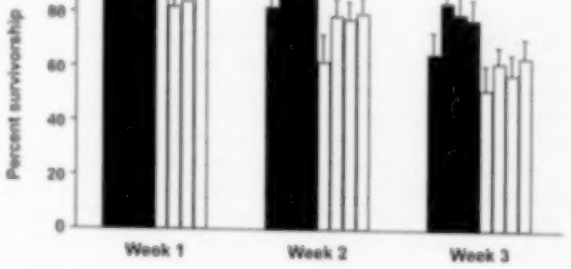
For spring–summer, PC1 correlated negatively with percent *G. pulex* and positively with ASPT, indicating that the invader decreased relative to the native in upland areas of the river system where the water was more oxygenated ($r = -0.59$, df = 23, $p < 0.01$), and this was reflected by changes in the wider macroinvertebrate assemblage, which became increasingly dominated by families sensitive to organic pollution ($r = 0.40$, df = 23, $p < 0.05$). PC2 and PC3 did not correlate significantly with either percent *G. pulex* or ASPT. For autumn–winter, PC3 correlated negatively with percent *G. pulex*, indicating that the invader decreased relative to the native as sites became faster flowing and more riffle dominated ($r = -0.48$, df = 23, $p < 0.05$).

Field transplant experiment

There was a strong trend for *G. d. celticus* survival in single-species tubes to vary among sites ($F_{[11,80]} = 2.0$, $p = 0.07$), with survivorship decreasing as the experiment progressed ($F_{[2,80]} = 107.5$, $p < 0.0001$). There was also a significant site × time interaction effect ($F_{[14,80]} = 2.5$, $p < 0.01$), as survivorship decreased slower in *G. d. celticus* only sites and faster in *G. pulex* only sites (Fig. 2).

In *G. pulex* only sites, *G. d. celticus* survivorship was significantly lower than that of *G. pulex* when held in single-species tubes ($F_{[1,40]} = 11.8$, $p < 0.01$) (Fig. 3*a*), and again, survivorship decreased as the experiment progressed ($F_{[2,80]} = 113.0$, $p < 0.0001$) (Fig. 3*a*). No other effects were significant. During weekly checks, it was noted that many

Fig. 2. Mean + SE percent survivorship of *G. d. celticus* in four single-species bioassay tubes after 1–3 weeks in situ in *G. d. celticus* only (solid bars) and *G. pulex* only (open bars) Lagan sites.



amphipod carcasses remained intact within tubes (approximately 80% of dead *G. d. celticus* and 70% of *G. pulex* recovered), indicating that physiological stress as opposed to cannibalism was responsible for deaths.

In mixed-species tubes, *G. d. celticus* survivorship was significantly lower than that of *G. pulex* ($F_{[1,20]} = 73.3$, $p < 0.0001$), with survivorship decreasing as the experiment progressed ($F_{[2,40]} = 56.6$, $p < 0.0001$). There was also a significant species × time interaction effect ($F_{[2,40]} = 4.4$, $p < 0.05$) (Fig. 3*b*), as *G. d. celticus* survivorship decreased at a much faster rate than that of *G. pulex*. At the end of 3 weeks, *G. d. celticus* survivorship was down to 16 ± 4% (mean ± SE) compared with 53 ± 5% for *G. pulex* in mixed-species tubes. Thus, *G. d. celticus* survivorship was a quarter of that when

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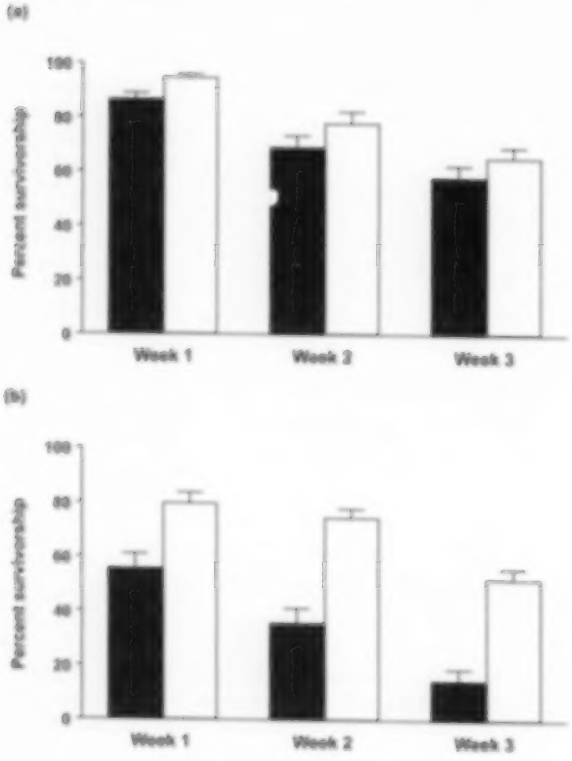
Fig. 3. Mean ± SE percent survivorship of *G. d. celticus* (solid bars) and *G. pulex* (open bars) amphipods in the transplantation experiment after 1–3 weeks in situ for (*a*) single- and (*b*) mixed-species bioassay tubes.



G. pulex was absent, while *G. pulex* mean survivorship was only 15% lower when *G. d. celticus* was present. During weekly checks, there were four instances of *G. pulex* observed killing *G. d. celticus* and only one of the reciprocal situation; numerous amphipod body parts were evident, indicating that IGP was occurring within tubes.

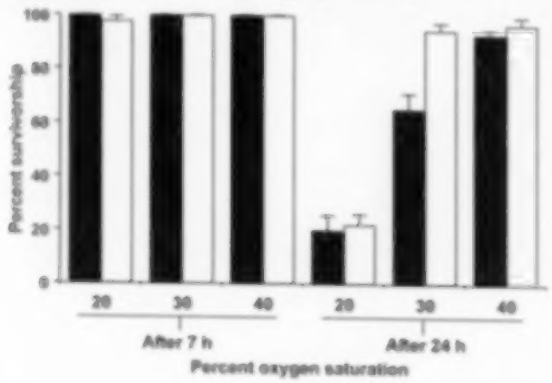
Although pH, conductivity, and current velocity did not significantly differ between *G. d. celticus* and *G. pulex* only sites ($F_{[1,6]}$ = 1.2, 1.0 and 1.3, respectively, all not significant), mean ± SE dissolved oxygen levels were higher in *G. d. celticus* sites than *G. pulex* sites (i.e., 8.79 ± 0.25 mg·L^{-1} compared with 7.30 ± 0.27 mg·L^{-1}; $F_{[1,6]}$ = 2.2, $p < 0.05$).

Laboratory experiments

Short-term oxygen tolerance experiment (single species)

Although overall amphipod survivorship decreased as percent oxygen saturation decreased and as the experiment progressed ($F_{[2,15]}$ = 151.1, $p < 0.0001$ and $F_{[2,15]}$ = 422.8, $p < 0.0001$, respectively), there was a significant species × oxygen level interaction effect ($F_{[2,15]}$ = 8.1, $p < 0.01$) and a species × oxygen level × time overall interaction effect ($F_{[2,15]}$ = 7.7, $p < 0.01$) (Fig. 4). Although *G. d. celticus* and *G. pulex* survivorships were similarly high after 7 h under all oxygen regimes, after 24 h at 20%, survivorships of both species were very low. At 30% saturation, *G. d. celticus* survivorship

Fig. 4. Mean ± SE percent survivorship of *G. d. celticus* (solid bars) and *G. pulex* (open bars) amphipods after 7 and 24 h in water of 20%, 30%, and 40% oxygen saturation.



was almost two thirds that of *G. pulex* (Fig. 4), and indeed, the latter's survivorship at 30% was little different from that at 40% saturation.

Longer term oxygen tolerance experiments (single and mixed species)

Gammarus d. celticus survivorship was lower at 40% than at 85% saturation ($F_{[1,28]}$ = 5.2, $p < 0.05$) and decreased faster at the lower saturation ($F_{[8,224]}$ = 2.6, $p < 0.01$) (Fig. 5*a*). At 85% saturation, there was a strong trend for *G. d. celticus* survivorship to be lower in the presence of *G. pulex* ($F_{[1,28]}$ = 4.0, p = 0.06), and indeed, survivorship decreased faster when *G. pulex* was present than when absent ($F_{[8,224]}$ = 10.2, $p < 0.0001$) (Fig. 5*a*). There was no interaction between oxygen saturation and *G. pulex* presence–absence on native survivorship. In addition to numerous *G. d. celticus* body parts present in mixed-species containers, there was one observation of an individual *G. d. celticus* being predated by two *G. pulex*.

Similar to the native, *G. pulex* survivorship was lower at 40% than at 85% saturation ($F_{[1,28]}$ = 4.8, $p < 0.05$) (Fig. 5*b*) and decreased fastest at the lowest saturation ($F_{[8,224]}$ = 2.6, $p < 0.01$) (Fig. 5*b*). In contrast, however, *G. pulex* survivorship was unaffected by the presence of *G. d. celticus* ($F_{[1,28]}$ = 0.3, not significant) (Fig. 5*b*), decreasing at the same rate whether the native was present or absent ($F_{[8,224]}$ = 1.0, not significant) (Fig. 5*b*). This was at 85% saturation, not at 40% saturation.

Discussion

Gammarus pulex has continued to replace *G. d. celticus* in the River Lagan, with only the invader now present in a high proportion of areas where the invader and the native once co-occurred. Earlier laboratory studies (e.g., Dick et al. 1993) implicated a biotic interaction (IGP) as the major determinant of invader and native distribution patterns in the Lagan. However, criticisms have been leveled at extrapolation of such laboratory observations to processes and distribution patterns in the field. Now via appropriate experimental field design (i.e., single- versus mixed-species tubes), we have provided evidence for differential IGP between *G. pulex* and *G. d. celticus* occurring within the environmental re-

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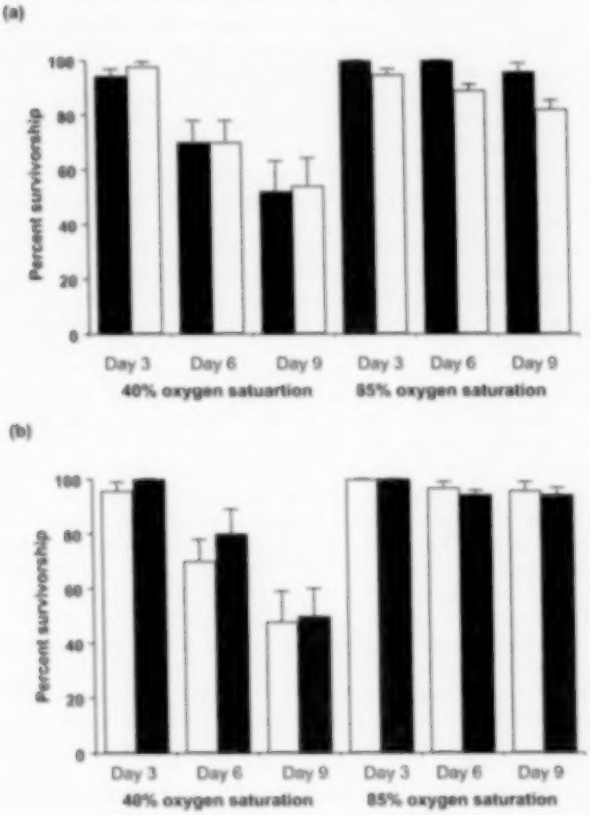
Fig. 5. Mean + SE percent survivorship of (*a*) *G. d. celticus* by itself (solid bars) and in the presence of the invader (open bars) and (*b*) *G. pulex* by itself (open bars) and in the presence of the native (solid bars) after 3–9 days in water of 40% and 85% saturation when only one or both species were present.



gimes of invaded river sites. Furthermore, via a combination of field survey and laboratory experiments, we have found that decreasing oxygen levels and water quality may favour replacement of the native by the invader because of differential physicochemical tolerance.

Our results imply that differential IGP in favour of *G. pulex* witnessed in previous laboratory studies under regimes favourable to both species (i.e., well oxygenated, filtered, 50%:50% mixes of native and invader source waters) is likely to be even more in favour of *G. pulex* in invaded sites in the field, where the native is under greater physiological stress than the invader. The lower survivorship of *G. d. celticus* in invaded sites, even with IGP excluded as a factor, implies that the native will always be excluded from such sites, unless water quality significantly improves. Given the current European situation where many rivers (including those in Northern Ireland) are environmentally degraded and increasingly stressed (Andrew 1998) once the native has been replaced in a site, there may be no way back. However, it should be noted that at the very lowest oxygen levels in our laboratory studies, *G. pulex* survivorship was as poor as that of *G. d. celticus*. Thus, if some of the invaded sites were increasingly deoxygenated, even *G. pulex* could be replaced by yet more tolerant invaders. For instance, in other areas of the Lagan that are grossly polluted and poorly oxygenated, *G. pulex* is absent and the hardier North American amphipod invader *Crangonyx pseudogracilis* now dominates (MacNeil et al. 2000*a*).

Despite the range expansion of *G. pulex*, it is intriguing that despite 13 years elapsing since the initial survey, native-only sites have remained native only, despite *G. pulex* sometimes being less than 2 km away for the whole of this period. This is surprising, as while our laboratory studies showed that native survivorship was lower than that of the invader at low oxygen levels, they also showed that native survivorship decreased in the presence of the invader in oxygen regimes that can be found in native-only sites. However, the situation in the Lagan is not unique, as Stock (1993) and Dick et al. (1997) noted that *G. pulex* had been unable to expand its range in areas where *G. d. celticus* dominated in Brittany and the Isle of Man, respectively. Meijering (1991) regarded *G. pulex* as a lowland species, and it is probable that our laboratory studies are oversimplified. We have concentrated on only one factor, dissolved oxygen level, as a determinant of distribution patterns, when a myriad of other physicochemical factors, perhaps related to the lowland or upland nature of sites, may be acting in conjunction to favour the native or prevent incursions of the invader. For instance, *G. d. celticus* is more tolerant than *G. pulex* of extremes in other environmental factors such as salinity (0.1–100‰) and temperature (5–15 °C) (Dennert 1974), and there are differences in physical habitat preference between the species that allow the coexistence of the two species within invaded lakes (Dick 1996; MacNeil et al. 2001*b*). Our study emphasizes that the genus *Gammarus* contains many species with different physiological tolerances as regards organic pollution (Walley and Hawkes 1996; MacNeil et al. 2000*a*). Many biotic indices of water quality such as the BMWP/ASPT system used in UK fresh waters (Biological Monitoring Working Party 1978), "lump" *G. d. celticus* and *G. pulex* together under the same Gammaridae score as regards sensitivity to pollution. In the current study, the native occurred with macroinvertebrate assemblages more sensitive to organic pollution, while the invader was found with less sensitive assemblages, indicating that using either *G. d. celticus* or *G. pulex* as the token Gammaridae could provide a false estimation of water quality. It must also be remembered that *Gammarus* spp. have been regarded as "keystone" species, impacting on different trophic levels in fresh water assemblages (Savage 1996). In particular, *G. pulex* is highly predatory to a range of macroinvertebrates also featured in biotic indices (Kelly et al. 2002), and species diversity has been found to be lower in *G. pulex* invaded sites (MacNeil et al. 2001*a*). Therefore, replacement of the less predatory native by the invader may have implications for the native macroinvertebrate assemblage as a whole and consequently biotic indices derived from them.

Many previous experimental transplant studies have been criticized, as they invariably reveal sources of mortality of species moved outside their normal physicochemical range but do not inform us about the reasons for the absence of species from certain areas (Strong et al. 1984). However, we have used transplants in a different way, reintroducing natives into areas where they had been replaced by the invaders

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and allowing natives to interact with invaders. Forys et al. (2001) highlighted the value of such an approach, especially when contemplating reintroductions of animals extinct in their native range. For instance, using seminatural enclosures, they found that predation by invasive fire ants was a likely cause of the decline and extinction of tree snails in parts of Florida. This knowledge could dictate areas where future snail reintroductions are likely to be successful. Given that many invasions, particularly in aquatic systems, accompany gradual environmental degradation or occur after restoration or a major disturbance (Conlan 1994; Van der Velde et al. 2002), field and laboratory studies that distinguish potential abiotic and biotic factors responsible for elimination of native species should be encouraged. This is vital if attempts at either preventing replacements of native species or reintroducing natives into invaded systems are to be successful.

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Appendix A

Table A1. Mean values (ranges in parentheses) of physicochemical and biological variables recorded in sites during spring–summer (upper value) and autumn–winter (lower value), where *G. d. celticus* only, *G. pulex* only, or both species were found.

Variable	*G. d. celticus* only	*G. pulex* only	Both species
Physical			
Slope of site (m·km^{-1}), L	125 (105–150)	90 (80–120)	110 (80–135)
Altitude of site (m), L	65 (20–100)	45 (10–90)	63 (50–100)
Mean wet width of channel (m), L	7.6 (2.5–11.3)	10.8 (3.2–15.0)	8.2 (1.5–12.0)
	9.1 (3.1–13.6)	14.5 (4.0–16.0)	9.4 (2.8–15.3)
Mean depth of water (cm), L	22.1 (8.5–36.0)	24.4 (23.8–30.0)	31.5 (12.0–54.0)
	32.6 (15.0–65.0)	34.9 (28.0–39.8)	39.9 (19.0–66.0)
Mean current velocity (m·s^{-1}), U	0.48 (0.40–0.57)	0.35 (0.06–0.41)	0.34 (0.00–0.46)
	0.55 (0.38–0.66)	0.39 (0.20–0.55)	0.37 (0.16–0.64)
% riffle in sampled area, A	90 (85–100)	65 (50–100)	65 (50–100)
	85 (0–100)	50 (0–100)	70 (0–100)
Substratum heterogeneity (1–7), U	5.0 (5)	5.5 (5–6)	5.4 (5–6)
	5.2 (5–6)	5.3 (4–6)	5.5 (4–6)
Mean substratum particle size (phi), U	−3.98 (−3.80 to −4.18)	−2.90 (−2.50 to −4.07)	−0.71 (6.50 to −6.50)
	−4.61 (−4.45 to −4.77)	−2.10 (−2.00 to −4.07)	−2.22 (6.50 to −6.40)
Minimum dominant particle size (phi), U	3.46 (4.00–3.12)	5.40 (6.50 to −2.00)	3.67 (6.50 to −2.00)
	3.16 (3.24–3.00)	5.70 (6.50 to −2.00)	2.86 (6.50 to −2.00)
Maximum dominant particle size (phi), U	−8.72 (−7.12 to −10.00)	−9.00 (−9.00)	−6.94 (2.50 to −9.00)
	−8.85 (−8.50 to −9.20)	−7.40 (−9.00)	−7.36 (2.50 to −9.00)
Modal dominant particle size (phi), U	−5.61 (−5.50 to −5.72)	−5.50 (−4.50 to −6.50)	−1.28 (6.50 to −6.50)
	−6.49 (−6.00 to −7.18)	−3.52 (4.50 to −6.50)	−3.46 (6.50 to −6.50)
Chemical			
Dissolved oxygen (mg·L^{-1}), U	9.91 (6.82–10.00)	6.83 (3.00–11.70)	7.88 (3.80–10.90)
	10.74 (10.44–12.48)	7.90 (5.91–12.80)	8.90 (6.8–13.10)
BOD_5, U	2.4 (2.0–2.6)	7.9 (3.0–9.5)	5.3 (2.9–5.6)
	1.3 (1.0–2.5)	6.5 (4.0–8.0)	6.0 (3.0–7.0)
Conductivity (μS·cm^{-1}), U	325 (97–340)	270 (73–320)	307 (97–340)
	239 (200–282)	200 (120–310)	265 (80–310)
pH, U	6.59 (5.9–8.96)	6.43 (5.30–8.60)	6.60 (5.90–9.15)
	6.44 (5.5–8.20)	6.12 (5.48–7.60)	6.13 (5.90–7.90)
Water temperature (°C), U	18.1 (16.2–18.0)	19.0 (15.5–21.0)	17.6 (15.0–20.0)
	4.5 (4.0–6.0)	5.1 (4.5–7.4)	5.2 (4.0–8.0)
Biological			
Tree canopy cover (%), A	20 (0–30)	15 (0–30)	10 (0–30)
	20 (0–30)	18 (0–40)	14 (0–30)
Mean macrophyte cover (%), A	20 (10–60)	25 (10–70)	15 (0–60)
	35 (20–60)	28 (10–60)	22 (0–60)
Mean litter cover of substrate (%), A	2.5 (0–5)	2.5 (0–5)	5.0 (0–10.0)
	18 (10–50)	20 (10–50)	20 (10–40)
ASPT, U	5.10 (4.60–6.15)	4.38 (3.20–4.63)	4.90 (3.80–5.21)
	5.45 (4.60–6.45)	4.60 (3.35–5.10)	5.00 (4.00–5.52)

Note: Transformations used for data analysis: A, arcsine; L, $\log(x + 1)$ or $\log(x)$ if x is never zero; U, untransformed data.

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Genome-size evolution in fishes

David C. Hardie and Paul D.N. Hebert

Abstract: Fishes possess both the largest and smallest vertebrate genomes, but the evolutionary significance of this variation is unresolved. The present study provides new genome-size estimates for more than 500 species, with a focus on the cartilaginous and ray-finned fishes. These results confirm that genomes are smaller in ray-finned than in cartilaginous fishes, with the exception of polyploids, which account for much genome-size variation in both groups. Genome-size diversity in ray-finned fishes is not related to metabolic rate, but is positively correlated with egg diameter, suggesting linkages to the evolution of parental care. Freshwater and other eurybiotic fishes have larger genomes than their marine and stenobiotic counterparts. Although genome-size diversity among the fishes appears less clearly linked to any single biological correlate than in the birds, mammals, or amphibians, this study highlights several particularly variable taxa that are suitable for further study.

Résumé : Les poissons possèdent à la fois les plus grands et les plus petits génomes des vertébrés, mais la signification évolutive de cette variation n'est pas encore comprise. Nous présentons des estimations de la taille du génome de plus de 500 espèces, en particulier de poissons cartilagineux et de poissons à nageoires à rayons. Nos résultats confirment que la taille du génome est plus petite chez les poissons à nageoires à rayons que chez les poissons cartilagineux, à l'exception des polyploïdes qui expliquent une partie importante de la variation de la taille du génome dans les deux groupes. La diversité de la taille du génome chez les poissons à nageoires à rayons n'est pas reliée au taux métabolique; il y a cependant une corrélation positive avec la taille des oeufs, ce qui laisse croire qu'il y a des liens avec l'évolution des soins parentaux. Les poissons d'eau douce et les poissons eurybiontes ont de plus grands génomes que leurs équivalents marins et sténobiontes. Bien que la diversité de la taille du génome chez les poissons semble moins clairement liée à une seul facteur biologique comme c'est le cas chez les oiseaux, les mammifères et les amphibiens, notre étude identifie plusieurs taxons particulièrement variables en vue d'études futures.

[Traduit par la Rédaction]

Introduction

Among vertebrates, genome-size measurements are available for approximately 400 amphibians (~8%), 320 mammals (~7%), 300 reptiles (~4%), 160 birds (~2%), and 900 fishes (~3%) (Gregory 2002*a*). Genome size is negatively associated with growth and development rate in varied organisms (e.g., Shuter et al. 1983; Chipman et al. 2001), while plants (Bennett 1976) and invertebrates (Cavalier-Smith 1978; Beaton and Hebert 1988) with larger genomes tend to exhibit broader ecological tolerance than those with lower DNA content. While genome size is negatively associated with metabolic rate in birds and mammals (Gregory 2002*a*), the evolutionary significance of genome-size diversity among reptiles and fishes is unresolved.

Genome-size diversity in fishes

Since the first broad studies of genome-size evolution among 275 bony fish species (Hinegardner 1968; Hinegardner and Rosen 1972), most work has concentrated on narrow taxonomic assemblages, with a strong bias towards freshwater species (data from Gregory 2001). Although each of these studies added taxonomic breadth to the data, these results have not been assembled to provide a broader overview of genome-size diversity in the fishes.

Low DNA content in ancestral chordates (e.g., Seo et al. 2001), and the multiplicity of certain gene families in vertebrates, which occur as single copies in their ancestral lineages, suggest that genome-duplication events have been important in the evolution of vertebrate genomes (e.g., Amores et al. 1998). The explosive speciation of teleosts may have been spurred by additional genome duplications after the divergence of the tetrapods (Amores et al. 1998), and additional "recent" polyploidization events account for the large genomes of many chondrichthyans (cartilaginous fishes) (Stingo and Rocco 2002) and chondrosteans (sturgeons and bichirs) (Blacklidge and Bidwell 1993), as well as certain actinopterygian (ray-finned) fishes (Uyeno and Smith 1972). Although fish genome sizes span the entire range of vertebrate DNA contents, being smaller than the smallest bird genome and bigger than the largest salamander genome, intraspecific variation, aside from ploidy shifts, is very low within most diploid fishes (e.g., Wolf et al. 1969; Tiersch and Goudie 1993).

Hinegardner and Rosen (1972) found that specialized fishes had smaller genomes than more generalized forms, and this trend was supported in later studies (Cimino 1974). This pattern may reflect decreases in chromosome number and ge-

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nome size in specialized species (Gold 1979), or constraints on genome size linked to the heightened developmental complexity of specialized species (Gregory 2002*b*).

Xia's (1995) model relating body temperature and gene duplication predicts that poikilotherms will have larger genomes in cold than in warm environments. Hardie and Hebert (2003) identified a trend towards larger cells in deep- and cold-water fishes, and a close correlation between genome and cell size in this group, results consistent with the finding that genome size increases with habitat depth among argentinoid fishes (Ebeling et al. 1971).

Species with large genomes also appear to survive better across a broader range of environmental variables (Gregory and Hebert 1999), and this pattern may also apply to fishes. This was first suggested as an explanation for the success of salmonid and catostomid fishes across broad latitudinal and salinity ranges (Allendorf and Thorgaard 1984). Nikolsky (1976) suggested that fishes in stenobiotic settings, such as marine and tropical waters, occupy narrow ecological ranges, while species from freshwater and temperate/polar climes occupy broad niches. He proposed that specialization in bony fishes has involved a move towards a narrower ecological amplitude and a decrease in chromosome number and genome size, which is supported by the small genomes of specialized fishes in stable environments (Uyeno and Smith 1972; Banerjee et al. 1988) and the larger genomes of fishes in broader niches (Ebeling et al. 1971).

The present study

This study provides genome-size estimates for more than 500 fish species. It focuses first on the range and variance of genome sizes within and among taxa, and this is followed by a consideration of the adaptive significance of these patterns. The taxonomic distribution of genome-size variance and the relative contribution of polyploidy are discussed, with a focus on chondrichthyan and actinopterygian fishes, as all new data are from these groups. Lastly, the evolution of fish genomes along physiological, developmental, and ecological gradients are considered.

Materials and methods

Sampling

Genome sizes were estimated in 1848 individuals representing 506 species from 155 families of marine and freshwater fishes, using Feulgen image analysis densitometry of erythrocyte nuclei from air-dried blood smears prepared as described elsewhere (Hardie et al. 2002). Blood smears from standard species (Siamese fighting fish, *Betta splendens*; goldfish, *Carassius auratus*; chicken, *Gallus domesticus*; rainbow trout, *Oncorhynchus mykiss*, and northern leopard frog, *Rana pipiens*) were collected as closely as possible to the time of sampling of unknowns.

Prior genome-size estimates for 54 agnathan, chondrichthyan, sarcopterygian, and cichlid fish species were also included to provide more comprehensive taxonomic coverage, producing a total of 560 species (Table D1[1]), using genome sizes from Gregory (2001) and karyotypes from Klinkhardt et al. (1995).

Metabolic rate data, corrected for body size and temperature (mg $O_2 \cdot min^{-1} \cdot kg^{-1}$ at 20 °C) and averaged over all species in a family for which data were available, were compiled from FishBase (2000) for 24 families for standard metabolism and for 37 families for routine metabolism. Egg-size data were compiled for 88 species of actinopterygian fishes (Coad et al. 1995; FishBase 2000). Reproductive modes were classified according to Baylis (1981), while taxonomy followed Nelson (1994).

Feulgen staining

Feulgen-stain preparation, dye manufacturer, lot number, and staining protocol were optimized as described in Hardie et al. (2002). The dye used was Sigma Basic Fuchsin Special for Flagella (B-0904, Lot 90K3681), and the protocol included 24 h fixation in 85 methanol : 10 formalin (37%) : 5 glacial acetic acid, 2 h room-temperature hydrolysis in 5 $mol \cdot L^{-1}$ hydrochloric acid, and 2 h staining time. Slides were stained in 1000-mL containers, with each run of 100 slides including at least one individual of each standard species and two individuals each of *G. domesticus* and *O. mykiss*. The strength of the correlation between staining intensity (integrated optical density) and the known genome sizes of the five standard species was tested for every run, and yielded highly significant and linear regressions ($r^2 > 0.95$, $P < 0.0001$). Genome sizes for unknowns were calculated based on the mean integrated optical density of the two *G. domesticus* smears), rather than from the standard curve (for justification see Hardie et al. 2002), using a "known" chicken genome size of 2.5 pg DNA per nucleus ($pg \cdot N^{-1}$) (Tiersch and Chandler 1989) for smears obtained from pathogen-free white leghorn hens from the Alma Poultry Research Station, Guelph, Ontario.

Data analysis

The Shapiro–Wilk test was used to test for normality of distributions. All data were log-transformed when required to achieve normal or near-normal distributions. Analysis of variance was used to compare means among groups, while the Kruskal–Wallis test was used to compare medians where outliers and (or) non-normality were a concern. Fisher's least significant difference test (multiple comparisons) and independent *t* tests (pairwise comparisons) were used to identify significant differences among group means. *F* tests were used to compare coefficients of variation (CVs) as described in Zar (1996). Data falling farther than 1.5 interquartile distances from the nonparametric 50th percentile range of any data set were identified as outliers. Least-squares regression and Pearson's correlation analysis were used to assess the strength of the relationships between genome size and both metabolic rate and egg diameter. While sufficient egg-size data were available to test this relationship at all taxonomic levels from species to order, metabolic-rate data were scarce, and could only be analyzed at the family level for families for which both genome-size and metabolic-rate data were

[1] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3604. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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available. The total variance attributable to each taxonomic level was determined by top-down variance component analysis (Sokal and Rohlf 1969). Statistical analyses were carried out using Excel + Analyze-It 2000 (Microsoft Corporation 2000), Sigmaplot version 4.0 (SPSS Inc. 1998), and Statgraphics Plus version 5.0 (Manugistics 1999).

The biological significance of some patterns of genome-size diversity for which sample sizes were unbalanced or too low to be tested statistically are nonetheless discussed to identify groups deserving of more thorough analysis in the future. Furthermore, phylogenetic relationships among fishes are poorly established, precluding analyses treating phylogenetic non-independence of data (i.e., phylogenetically independent contrasts).

Results

Genome-size diversity among fish classes

Significant differences in both median (Kruskal–Wallis test, $P < 0.05$) and mean (analysis of variance, $P < 0.05$) genome sizes ($\log_2$-transformed) occurred among the five fish classes. In fact, differences among classes accounted for more than 93% of the total variance in genome size among fishes (Fig. 1; Table 1). Log-transformation of genome sizes normalized data for all classes (Shapiro–Wilk test, $P > 0.67$) except the actinopterygians, sarcopterygians, and lampreys ($P < 0.05$). Fisher's least significant difference test confirmed that the means for all five classes differed significantly from each other ($P < 0.05$). Since the data for the hagfishes, lampreys, and sarcopterygian fishes were taken from the literature, these groups are not discussed further, except to note the significantly larger genomes of the direct-developing hagfishes (6.6 pg·N^{-1}) relative to the metamorphosing lampreys (3.0 pg·N^{-1}), and the massive genomes of the lungfishes (80.9–225.6 pg·N^{-1}) relative to the coelacanth (7.2 pg·N^{-1}). Genome sizes of species in the three classes of primitive fishes (hagfishes, lampreys, chondrichthyans) appeared to vary in a quantum series, with multiples of 2.9 pg·N^{-1} in the hagfishes and lampreys and multiples of 1.45 pg·N^{-1} in the chondrichthyans.

Genome-size diversity among chondrichthyans

The distribution of chondrichthyan genome sizes extended across a broad range (~30 pg·N^{-1}, CV 55%), and was significantly skewed around a mean of 11.8 pg·N^{-1} (Shapiro–Wilk test, $P < 0.0001$). Variance among orders within this class (42.5%) and among families within orders (41.7%) accounted for similar amounts of the total genome-size variance, while variance among (8.1%) and within (3.7%) genera was much less important (Table 1). A high degree of variance in genome size among chondrichthyan families and orders was evident (Table 1), but its statistical significance could not be tested because some orders were represented by single families. A large component of the total variance within orders was due to broad ranges within such orders as the Carcharhiniformes (6.1–13.0 pg·N^{-1}), Squaliformes (11.6–22.5 pg·N^{-1}), and Rajiformes (5.6–10.8 pg·N^{-1}). Variable families contributing to the intergeneric variance component included the hound sharks (Triakidae; 8.6–17.3 pg·N^{-1}) and the rays (Dasyatidae; 8.3–13.4 pg·N^{-1}).

Genome-size diversity among actinopterygians

Genome sizes in actinopterygians ranged from a low of 0.8 pg·N^{-1} in the pufferfish *Canthigaster benneti* to a high of 13.8 pg·N^{-1} in the shortnose sturgeon, *Acipenser brevirostrum*, and showed a significant deviation from normality (Shapiro–Wilk test, $P < 0.0001$) around a mean of 2.0 pg·N^{-1}. The CV in genome size among species (52%) did not differ significantly from that in chondrichthyans (F test, $P > 0.05$). This study largely examined marine species, and the addition of previous data for freshwater taxa (from Gregory 2001) raised the mean to 2.4 pg·N^{-1}, although it was still significantly negatively skewed (Shapiro–Wilk test, $P < 0.0001$).

Genome-size variation among actinopterygians

Variance among actinopterygian orders accounted for 80% of the total variance in this class, while families and genera did not contribute further variance, and variance among congeneric species and intraspecific variance contributed approximately 16.7% and 3.1% to the total variance, respectively (Table 1). The high variance among orders was mostly due to the inclusion of orders dominated by polyploids, such as the Acipenseriformes, Salmoniformes, and Cypriniformes. Some polyploid genera, such as *Acipenser* (4.4–13.8 pg·N^{-1}), also contributed to variance at the generic level, while neopolyploid specimens of *Acipenser brevirostrum*, *Acipenser oxyrhynchus*, *Salmo salar*, and *Phoxinus neogaeus* contributed to intraspecific variance. The exclusion of these polyploid orders halved the ordinal contribution to total variance, producing a genome-size distribution with a closer approach to normality, with each higher taxonomic level contributing successively more variance (Table 1). Although the distribution of actinopterygian genome sizes still deviated from normality when the three polyploid orders were excluded (Shapiro–Wilk test, $P < 0.0001$), the data were significantly less variable (CV 32%, F test, $P < 0.05$) around a significantly lower mean of 1.8 pg·N^{-1} (t test, $P < 0.005$). All significant actinopterygian outliers were large-genome species, and most were polyploid (Fig. 2).

Genome-size diversity among conspecifics was ordinarily low, with a CV less than 10% for 387 of 398 species (Fig. 3). Three high outliers derived from the detection of neotriploids in aquaculture strains (*A. brevirostrum*, *A. oxyrhynchus*, *S. salar*) and intraspecific ploidy differences in several other species (e.g., *Synodontis notatus* and *P. neogaeus*). Other cases where single individuals had genome sizes deviating significantly (one-sample t test, all $P < 0.05$) from those of their conspecifics included the green jobfish (*Aprion virescens*), golden toadfish (*Lagocephalus lunaris*), the blue devil (*Chrysiptera cyanea*), gelatinous snailfish (*Liparis fabricii*), orange roughy (*Hoplostethus atlanticus*), and broadbill swordfish (*Xiphias gladius*).

Members of most fish families showed little variation in genome size, with CVs lower than 20% (Fig. 4). However, 12 of the 87 families had CVs greater than 20%, including representatives from three classes: Myxini, Chondrichthyes, and Actinopterygii. High CVs in the Myxinidae reflected the non-overlapping ranges of genome size between members of the subfamilies Myxininae (8.6–9.2 pg·N^{-1}) and Eptatretinae (4.6–6.9 pg·N^{-1}). Chondrichthyan families with broad ranges of genome size included the requiem sharks (Carcharhinidae, 5.7–9.9 pg·N^{-1}), stingrays (Dasyatidae, 6.8–13.4 pg·N^{-1}),

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Fig. 1. Distribution of genome sizes among 560 species belonging to five classes of fishes. (*a*) The Myxini (7 species; open bars) and Cephalaspidomorphi (8 species; solid bars). (*b*) The Chondrichthyes (47 species). (*c*) The Sarcopterygii (5 species). (*d*) The Actinopterygii (493 species). Data derived from this study (506 species) and published data (54 species) were used to ensure coverage of all major taxonomic groups.

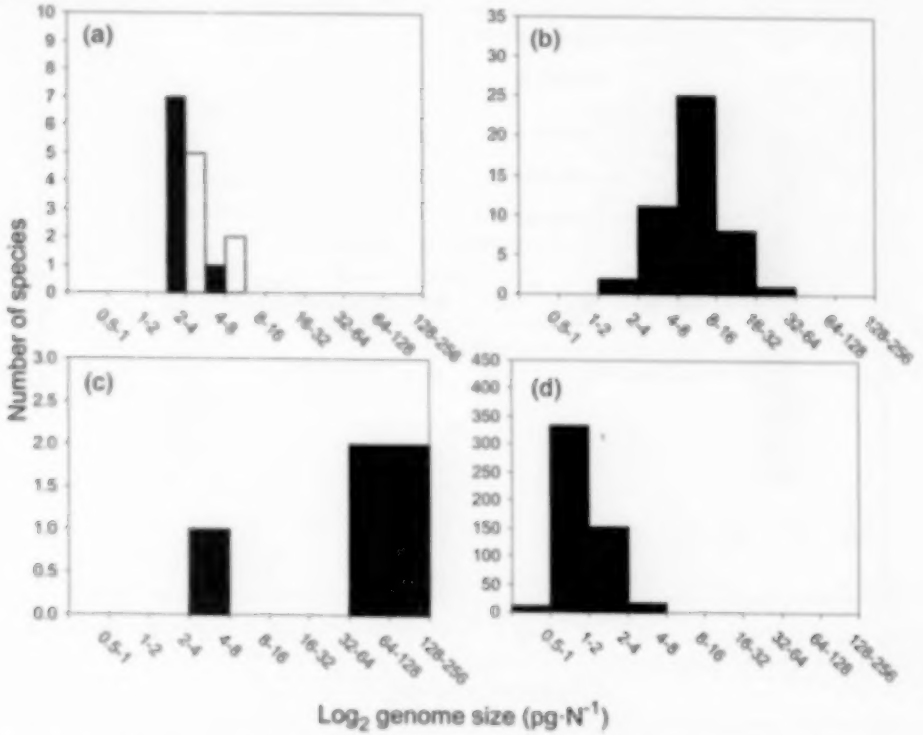

Table 1. Variance component analysis showing the portion of total variability in fish genome size contributed by each taxonomic level.

	Percentage of variance			
Source of variance	Entire data set	Chondrichthyans	All actinopterygians	Diploid actinopterygians
Class	93.78	—	—	—
Order	3.58	42.46	80.15	42.03
Family	2.44	41.71	0.00	31.43
Genus	0.00	8.06	0.00	15.96
Species	0.17	3.74	16.72	7.70
Individual	0.03	0.23	3.13	2.87

Note: Zero values indicate that no variance was added at a given taxonomic level that was not already accounted for at higher levels.

and hound sharks (Triakidae, 8.6–17.3 pg·N^{-1}). Among actinopterygian families, the acipenserids (4.4–13.8 pg·N^{-1}) and cyprinids (2.2–3.4 pg·N^{-1}) had broad ranges of genome size that reflect interspecific differences in ploidy level. By contrast, entirely tetraploid families, such as the salmonids and catostomids, had lower CVs, reflecting narrower ranges. Genome sizes also ranged widely in six diploid actinopterygian families: the pipefishes and seahorses (Syngnathidae, 1.2–2.7 pg·N^{-1}), dories (Zeidae, 1.5–2.5 pg·N^{-1}), dragonets (Callionymidae, 1.4–2.0 pg·N^{-1}), wrasses (Labridae, 1.3–2.8 pg·N^{-1}), filefishes (Monacanthidae, 0.9–1.6 pg·N^{-1}), and silversides (Atherinidae, 1.3–2.1 pg·N^{-1}), all of which had CVs greater than 20%.

Physiological, reproductive, and ecological correlates of genome-size diversity among the actinopterygians

There was no significant relationship between the mean genome size of species in a fish family and either standard (24 families, $r^2 = 0.02$, $P > 0.45$) or routine (37 families, $r^2 = 0.007$, $P > 0.73$) metabolic rates (Fig. 5). However, a strong positive relationship was identified between genome size and egg diameter in actinopterygians (Fig. 6). The relationship persisted at the specific ($r^2 = 0.30$), generic ($r^2 = 0.29$), familial ($r^2 = 0.15$), and ordinal ($r^2 = 0.41$) levels (all $P < 0.007$). Actinopterygian families showing parental care also had larger genomes (mean = 2.48 pg·N^{-1}) than nonguarding open-substratum scatterers (mean = 1.79 pg·N^{-1})

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Fig. 2. Box-whisker plot of actinopterygian genome sizes. The box indicates the non-parametric 50th percentile range and is divided at the median. The outer lines indicate the 95th percentile range. Outliers, indicated by points on the graph, are more than 1.5 interquartile ranges (1 interquartile ranges = 0.67 pg) outside the 50th percentile range. Significant outliers include both polyploid (○) and diploid (●) species.

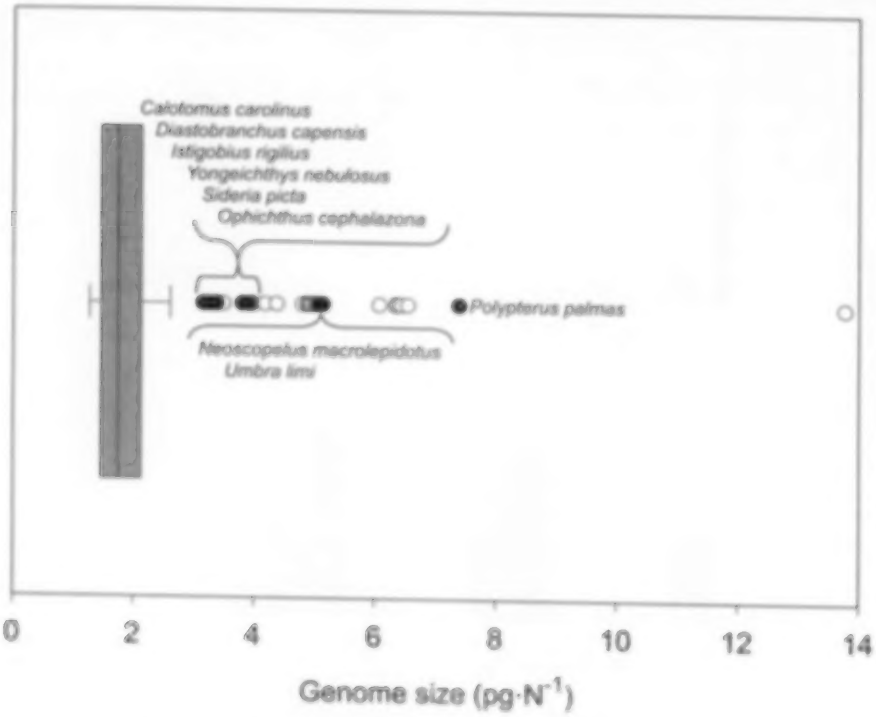

Fig. 3. Relationship between coefficient of variation (CV) and genome size for all 398 fish species from the present study represented by two or more individuals. Species identity is shown for both polyploid (○) and diploid (●) taxa with CVs greater than 10%.

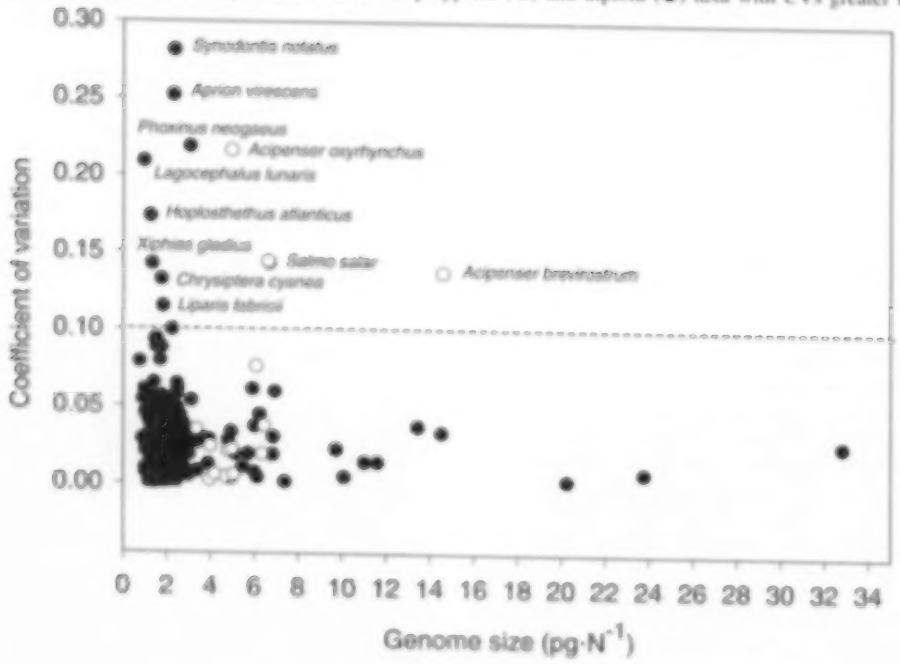

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Fig. 4. Relationship between CV and genome size among all 87 fish families represented by two or more species. Identity is shown for 12 families with CVs greater than 20% and for 2 less-variable polyploid families (○).

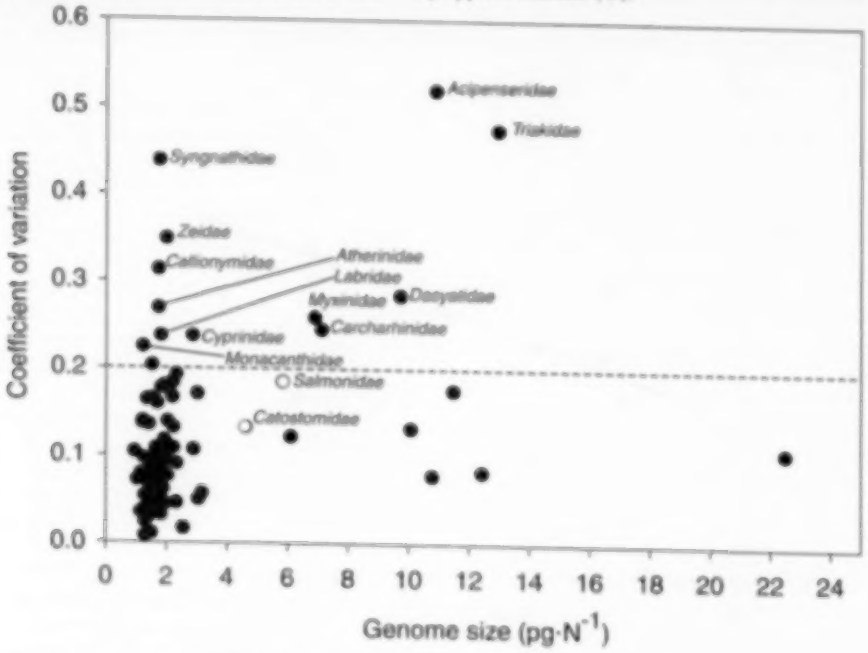

Fig. 5. Relationships between mean standard (●, solid line; $n = 24$, $r^2 = 0.016$, $P > 0.55$) and routine (○, broken line; $n = 37$, $r^2 = 0.002$, $P > 0.81$) metabolic rates and mean genome size for all fish families represented in this study for which metabolic-rate data are available in FishBase (2000).

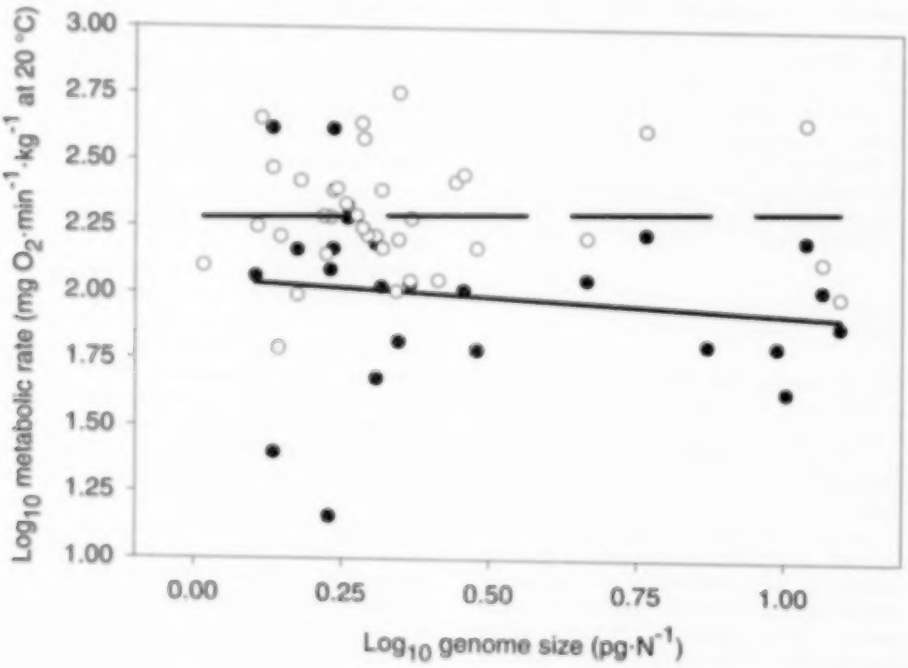

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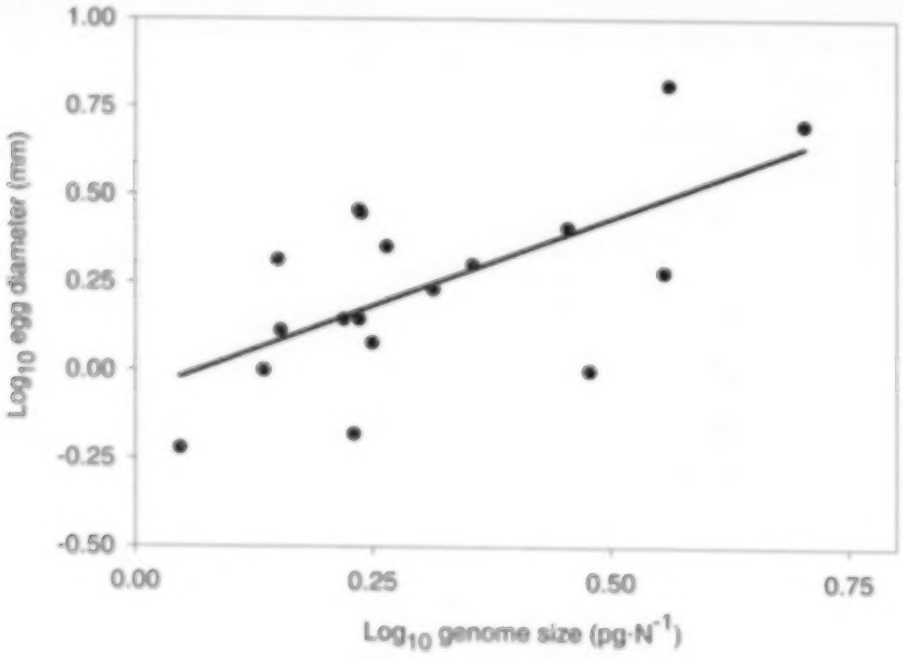
Fig. 6. Relationship between mean egg diameter and genome size for 18 orders of actinopterygian fishes ($r^2 = 0.41$, $P < 0.005$). These results derive from the analysis of 88 species. The regression persists (all $P < 0.007$) at the specific ($r^2 = 0.30$), generic ($r^2 = 0.29$), and familial ($r^2 = 0.15$) levels.



(Table 2; t test, $P < 0.0006$). Furthermore, the data provide many specific examples of significantly larger genomes in species that exhibit a higher degree of parental care than their allies (Hardie 2002).

Interestingly marine/catadromous actinopterygians had significantly smaller genomes (mean = 1.77 pg·N^{-1}) than their freshwater/anadromous counterparts (mean = 2.81 pg·N^{-1}; t test, $P < 0.0001$). Polyploidy in actinopterygians was limited to freshwater/anadromous taxa, but the significantly larger genomes of freshwater fishes persisted even with their exclusion (freshwater diploid mean = 2.32 pg·N^{-1}; t test, $P < 0.0001$).

Discussion

Genome-size diversity among fish classes

This study has confirmed that there are large differences in genome size among the five fish classes. The 36-fold range of genome size among sarcopterygian fishes is due mostly to the remarkably large genomes of the lungfishes, which provide evidence of a major shift in genome size within this class, unrivalled by any other group of animals. Although most of this apparently occurred as a result of polyploidy (Klinkhardt et al. 1995), the low chromosome numbers (~38) of most dipnoans make it unlikely that polyploidy alone accounts for the high DNA contents of this group. The genomic obesity of lungfishes has been linked to aestivation (Cavalier-Smith 1978), but this association will be difficult to validate, given the low species diversity of this group. The non-overlapping genome sizes of the direct-developing hagfishes (4.6–9.2 pg·N^{-1}) and the metamorphosing lampreys (2.6–4.2 pg·N^{-1}) provide a potential example of genome-size constraint linked to developmental complexity.

The present study has revealed evidence that genome sizes in primitive fishes vary in a quantum series (for a more complete discussion see Hardie 2002). This observation justifies further investigation, since the genomes of several other groups of organisms evolved as multiples of some "basal" C value (e.g., Narayan 1985).

Genome-size diversity: chondrichthyans versus actinopterygians

The high mean, broad range, and discontinuous variation of genome sizes of chondrichthyans relative to those of actinopterygians support earlier reports that polyploidization followed by rediploidization characterizes genome-size evolution in this group (Stingo and Rocco 2002). Although large-scale differences in genome size among chondrichthyan orders contribute much variation, intergeneric variation within families can also be significant. In contrast, polyploidy is less common among ray-finned fishes, where diploid chromosome numbers remain remarkably constant around 48, even among species that differ significantly in DNA content (Klinkhardt et al. 1995). The fact that DNA content has evolved differently between cartilaginous and ray-finned fishes is not surprising, given that the classes differ drastically in traits such as physiology, reproduction, and development, and have had longer histories of evolutionary independence than most other vertebrate classes. Nucleotypic limitations of genome size on cellular and organismal phenotypes may explain why the chondrichthyans, with their slow and direct development, viviparity, long life-span, low

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Table 2. Mean genome size and reproductive mode for 22 freshwater and 18 marine families of fishes that are primarily larva guarders (L), embryo guarders (E), and bearers (B; includes mouthbrooders).

Family	Mode of parental care	Mean genome size ($pg \cdot N^{-1}$)
Freshwater habitat		
Characidae (characins)	B	3.00
Adrianichthyidae (adrianichthyids)	B	1.95*
Poeciliidae (mollies)	B	2.76
Osteoglossidae (bonytongues)	B, E	1.69
Loricariidae (armoured catfishes)	B, E	3.15
Doradidae (thorny catfishes)	E	3.20*
Siluridae (sheatfishes)	E	2.18*
Cyprinidae (carps)	E	2.85
Notopteridae (knifefishes)	E	3.38
Callichthyidae (armoured catfishes)	E	4.82
Umbridae (mudminnows)	E	5.13
Salmonidae (salmonids)	E	5.27
Fundulidae (topminnows and killifishes)	E	2.58
Eleotridae (sleepers)	E	2.50
Belontiidae (gouramies)	E	1.28
Cichlidae (cichlids)	B, L	2.33
Amiidae (bowfins)	L	2.28
Ictaluridae (North American catfishes)	L	2.08*
Channidae (snakeheads)	L	1.62*
Gasterosteidae (sticklebacks)	L	1.30
Centrarchidae (sunfishes)	L	1.92
Ophidiidae (cusk-eels)	B	1.23
Marine habitat		
Scorpaenidae (scorpionfishes and firefishes)	B	2.21
Syngnathidae (seahorses & pipefishes)	B	1.74
Opistognathidae (jawfishes)	B	2.12
Apogonidae (cardinalfishes)	B	2.03
Hemirhamphidae (halfbeaks)	B	2.22
Embiotocidae (surfperches)	B	1.68*
Cottidae (sculpins)	B, E	1.66
Ariidae (ocean catfishes)	B, E	4.94
Plotosidae (eel-tailed catfishes)	E	3.49
Cyclopteridae (lumpfishes)	E	1.81
Batrachoididae (toadfishes)	E	5.33*
Sparidae (porgies)	E	1.40
Labridae (wrasses)	E	1.80
Zoarcidae (eelpouts)	E	1.93
Stichaeidae (pricklebacks)	E	1.60
Blenniidae (blennies)	E	1.35
Gobiidae (gobies)	E	2.33
Tetraodontidae (pufflers)	E	0.94

Note: Classification of reproductive modes follows Baylis (1981). Genome sizes are from this study except for those marked with an asterisk, which are from Gregory (2001).

metabolic rate, and large body size, have evolved larger genomes than the actinopterygians, which generally fall at the other end of the spectrum with respect to these features.

Genome-size diversity among actinopterygians: the role of polyploidy

The current data confirm the fact that much genome-size variation among actinopterygians stems from polyploidy. In fact, the broad ranges of genome sizes of species within the four orders that contain polyploid taxa (Acipenseriformes, Cypriniformes, Siluriformes, Salmoniformes) account for much of the total variation among actinopterygian genomes. The higher CVs of the acipenserid and cyprinid families versus the salmonids and catostomids reflect the fact that species in the former families show ploidy variation (e.g., Blacklidge and Bidwell 1993; Gold and Li 1994), while the latter are all tetraploid (e.g., Allendorf and Thorgaard 1984; Uyeno and Smith 1972). Likewise, the highest CVs at both inter- and

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intra-specific levels were largely due to ploidy-level differences. Particularly high CVs were observed among species of *Acipenser*, which show evidence of one to four polyploidization events from a diploid ancestor represented by the extant *Huso dauricus* (Blacklidge and Bidwell 1993). Since sturgeon species with genome sizes around 4.5 pg·N^{-1} are octaploid (~120 chromosomes; Blacklidge and Bidwell 1993), it is likely that *A. oxyrhynchus* (4.4 pg·N^{-1}) is also octaploid, while *A. brevirostrum* (13.8 pg·N^{-1}) is dodecaploid (~360 chromosomes). The reasons why dramatic ploidy increases have been tolerated in this order are unclear, since the 6-fold range of DNA contents among acipenseriform species is not related to any conspicuous biological correlate.

Genome-size diversity among putative diploid actinopterygians

The mean and range of actinopterygian genome sizes observed in this study are similar to those reported by Hinegardner and Rosen (1972). Once polyploid orders were excluded, the ordinal variability of actinopterygian genome sizes was halved, and family and generic variability became significant. Large interspecific genome-size differences within both the seahorse and pipefish subfamilies account for the high CV of the syngnathid family. Although a four-fold range has previously been reported among different pipefish species (Vitturi et al. 1998), this is the first report of similar differences among seahorses, which were previously thought to have small genomes (Hinegardner 1968; Vitturi et al. 1998). The high CVs discovered within other diploid actinopterygian families, such as the zeids, callionymids, and atherinids, require further investigation, as each of these families was represented by only two species. Previous evidence for intrafamily variation has been limited to polyploid taxa (e.g., Wolf et al. 1969; Allendorf and Thorgaard 1984), while diploid fish families generally have CVs lower than 20% (e.g., Hinegardner and Rosen 1972; Tiersch and Goudie 1993), which is similar to most results in this study.

Divergent actinopterygian genomes

Although most of the positive genome size outliers among actinopterygians were polyploids, some diploid outliers possessed physiological, reproductive, or ecological attributes that may explain their unusual genome sizes. The large genome of the bichir, *Polypterus palmas*, is consistent with suggestions that slowly evolving groups have larger genomes than rapidly evolving ones (Hinegardner and Rosen 1972). Polyploidy is an unlikely explanation in this case, given this group's low chromosome number (36; Klinkhardt et al. 1995). Similarly, the large genome of the mudminnow, *Umbra limi*, is remarkable, since this species has a diploid chromosome number of just 22, while its European congener *Umbra krameri* has 44 chromosomes (Klinkhardt et al. 1995). Moreover, its North American relatives, *Novumbra hubbsi* and *Dallia pectoralis*, have genomes half as large, despite having 48 and 78 chromosomes, respectively (Beamish et al. 1971).

The large genomes of some gobiids, like the large genome of the mouth-brooding catfish, *Arius gruffei*, may reflect their high degree of parental care. The high DNA content in the latter species is consistent with an earlier report (Hinegardner and Rosen 1972) of large genomes among ariids, and there are no reports of polyploidy in this family. The large genome of the lanternfish *Neoscopelus macrolepidotus* is consistent with Ebeling et al.'s (1971) report of large genomes in deep-water myctophids, which may be relevant to these species' broad ecological amplitudes, as they undertake extensive vertical migrations daily.

Physiological correlates of genome-size diversity among actinopterygians

At first consideration, the massive genomes of aestivating lungfishes appear to represent a prime example of metabolic constraints on genome size in poikilothermic vertebrates (Cavalier-Smith 1991), as do the large genomes of fishes able to survive in oxygen-depleted waters, or even out of water altogether, such as *U. limi* (present study), as well as the rivulines and killifishes relative to other cyprinodontiforms (~3 vs. ~1.8 pg·N^{-1}; Hinegardner and Rosen 1972). However, several extremely active fish groups, including scombrids, xiphids, and salmonids, have genomes similar in size or larger than those of sluggish species such as flatfishes and syngnathids. Furthermore, Pauly et al. (2000) found no evidence for a negative association between DNA content and caudal-fin aspect ratio (as a measure of activity / metabolic rate) in fishes. The lack of a significant relationship between metabolic rate and genome size in fishes agrees with results obtained in studies on other poikilotherms (e.g., Licht and Lowcock 1991). In general, these trends suggest that metabolic constraints on genome size are weak in fishes, except possibly the cartilaginous fishes, which have much lower metabolic rates than bony fishes (Brett 1970).

Reproductive correlates of genome-size diversity among actinopterygians

Given the strong positive association between genome and erythrocyte sizes in fishes (Hardie and Hebert 2003), it is not surprising that egg diameter is positively correlated with genome size in actinopterygians. Moreover, this relationship has particular ecological significance, since the production of large eggs limits fecundity and is associated with parental care (Sargent et al. 1987). As predicted by these associations, a large genome was also typically linked to parental care in fishes. Interestingly, genomes are generally larger in freshwater than in marine fishes, and the former tend to show a higher degree of parental care (Breder and Rosen 1966). These results may provide the first example of a genome-size-driven shift into a "novel niche" among fishes (Gregory and Hebert 1999). Since genome size is clearly related to egg size in fishes, large increases in DNA content might result in intense selection for increased parental care, to compensate for decreased fecundity. This trend is similar to the case of brain and feeding behaviour simplification in some amphibians after the expansion of their genomes (Roth and Wake 2001).

If high DNA content coevolved with parental care in fishes, the paucity of large genomes and the negative skew of DNA contents are consistent with the fact that most fish families (~77%) show no parental care. By comparison, about 17% care for eggs, while 6% extend this care to newly hatched young (Keenleyside 1978). The internal fertilization and slow, direct development of chondrichthyans versus the usual ovi-

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parity, external fertilization, and rapid development of actinopterygians provides general evidence for reproductive and developmental correlates of genome-size differences between classes. Thus, as noted in other poikilotherms (e.g., Chipman et al. 2001), nucleotypic effects of genome size on cytological parameters are most strongly exhibited as constraints on early development in fishes. Hence, it is possible that an increase in genome size has driven the evolution of viviparity and parental care in certain fish lineages. However, some continuous quantifiable measure of development rate is needed to test whether genome size limits it directly.

Ecological correlates of genome-size diversity among actinopterygians

The fact that freshwater/anadromous have larger genomes than marine/catadromous actinopterygians supports the prediction that eurybiotic fishes will have larger genomes than stenobiotic fishes (Ebeling et al. 1971), and is consistent with evidence that large-genome organisms have broader ecological tolerances (Bennett 1976; Beaton and Hebert 1988). The present study has revealed other evidence that a high DNA content may be linked to ecological factors in vertically migrating myctophids and taxa routinely exposed to harsh environments, such as umbrids, dipnoans, fundulids, and poeciliids.

The adaptive advantage of gene multiplicity in polyploids has previously been advanced as an explanation for their relative success and frequency in stochastic freshwater systems (Ebeling et al. 1971; Allendorf and Thorgaard 1984). While these factors may explain the persistence of polyploid lineages in freshwater/anadromous fishes, it is also possible that polyploids simply arise more often in these settings. Relative to the marine environment, where few barriers limit gene flow, the freshwater environment is highly dissected, providing more opportunities for population isolation, a factor that may enhance opportunities for the synthesis of polyploids (Otto and Whitton 2000).

Although the larger genomes of freshwater fishes reflect, in part, the greater prevalence of polyploids in these settings, diploid genomes are still larger in freshwater/anadromous than in marine/catadromous actinopterygians. Furthermore, polar marine fishes have smaller-than-expected genomes, which may relate to the fact that their environment, although extreme, is highly stable, barring seasonal fluctuations in productivity. Similarly, the fact that tropical marine taxa have small genomes is consistent with their occupancy of stable environments. Thus, although the precise mechanisms underlying the elevation of genome size in freshwater/eurybiotic versus marine/stenobiotic fishes remain unknown, these results support previous suggestions that genome size and ecological amplitude are positively related in fishes (Ebeling et al. 1971; Nikolsky 1976), as in other groups (Beaton and Hebert 1988).

The relatively small genomes of cold-water fishes conflict with the prediction (Xia 1995) that cold-climate poikilotherms will have larger genomes than their warm-climate counterparts. The small genomes of polar fishes may be explained by development-time constraints imposed by the ephemerality of growth seasons, which may select for high rates of larval development, and therefore small genomes. Moreover, fishes chronically exposed to low temperatures may have evolved compensatory mechanisms (e.g., larger yolk supplies) to overcome environmental challenges. However, the lack of any consistent trend suggests that thermal regime is not strongly related to DNA content in fishes, in contrast to clinal patterns in other groups (Bennett 1976; Xia 1995).

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A recipe for Bayesian network driven stock assessment

T.R. Hammond

Abstract: Markov Chain Monte Carlo (MCMC), the most widely used algorithm in Bayesian statistics, can fail to converge. Although convergence is tested by various diagnostics, these can only reveal failure, never success. To avoid these difficulties, this paper suggests a recipe for using Bayesian network propagation (BNP) to compute posterior results for fish stock assessment. Bayesian networks employ discrete random variables and specify relationships between them with conditional probability tables. Therefore, the recipe uses a new technique called "fuzzy discretization" to convert a continuous Bayesian model into a discrete Bayesian network. The technique is illustrated on a Schaefer assessment model by showing how model equations can be converted to probability tables. Posterior density estimates for carrying capacity (K) from both MCMC and BNP were compared with exact results (obtained by analytic integration and grid search) under three scenarios. BNP outperformed MCMC (as implemented in WinBUGS) in all scenarios, though MCMC diagnostics previously deemed sufficient reported no problems. Tightening the grid resolution of discrete numeric variables over regions of high posterior probability greatly improved BNP performance, so a grid selection heuristic is included in the recipe. In summary, this recipe may provide an effective alternative to MCMC for similar Bayesian problems.

Résumé : L'algorithme Monte Carlo par chaine de Markov (MCMC), le plus communément utilisé dans les méthodes bayésiennes, peut ne pas converger. Bien qu'il existe diverses méthodes diagnostiques pour évaluer la convergence, celles-ci n'indiquent que le manque de convergence, jamais sa présence. Pour éviter ces problèmes, une méthode est suggérée ici pour utiliser un réseau de propagation bayésien (BNP) pour calculer les résultats a posteriori pour l'évaluation des stocks de poissons. Les réseaux bayésiens utilisent des variables aléatoires discrètes et précisent les relations entre elles au moyen de tables de probabilité conditionnelle. La méthode utilise donc une nouvelle technique, la discrétisation floue, pour convertir un modèle bayésien continu en un réseau bayésien discontinu. Une démonstration de la transformation des équations du modèle d'évaluation de Schaefer en tables de probabilité sert d'illustration à la méthode. Les estimations a posteriori de la densité du stock limite (K) obtenues par MCMC et BNP sont comparées aux résultats précis (obtenus par intégration analytique et recherche de grille) sous trois scénarios. BNP fonctionne mieux que MCMC (appliqué à l'aide de WinBUGS) dans tous les scénarios, bien que les outils diagnostiques considérés jusqu'à maintenant adéquats n'aient signalé aucun problème. Le resserrement de la résolution de la grille des variables numériques discrètes dans les régions de forte probabilité a posteriori améliore considérablement la performance de BNP; une méthode heuristique de sélection de la grille est donc incluse dans la méthodologie. En bref, cette méthodologie peut fournir une alternative efficace à MCMC pour des problèmes bayésiens de nature similaire.

[Traduit par la Rédaction]

Introduction

Bayesian analyses convey uncertainty about parameters of interest with probability distributions. Prior distributions (priors) represent knowledge available before observing a set of data, and a joint posterior distribution (for all parameters together) represents the state of knowledge afterwards. By Bayes' theorem, the posterior distribution is proportional to the product of the likelihood function for the data and the priors. Typically, the results of a Bayesian analysis are presented using the marginal posterior distributions of individual parameters.

The Bayesian approach has several advantages. It is compellingly concise; all essential theory is contained in the previous paragraph. It conveys uncertainty clearly (Punt and Hilborn 1997), is suited to learning from experience (Liermann and Hilborn 1997; Hammond and Ellis 2002), and lends itself to Bayesian decision analysis (McAllister and Kirkwood 1998*a*, 1998*b*), an accessible approach to evaluating the consequences of alternative management actions (Varis and Kuikka 1999).

With such advantages, the Bayesian approach might have taken over fisheries science altogether, but it has not. Though obtaining priors may be daunting, the difficulties with implementation have most prevented progress.

Implementation problems arise because computing the constant of proportionality in Bayes' theorem often involves an

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intractable integration. In problems with few variables, the grid search method can circumvent the difficult computations. In this approach, the posterior is evaluated over a grid of parameter values, despite the unknown constant of proportionality. Normalizing these computed values so that they sum to one over the grid yields a probability table from which marginal posterior results are readily computed. In general, the marginal probability tables computed in this way are not exact (accuracy is a function of grid range and resolution), but when there is only one variable, they are. In that case, the true marginal posterior density, evaluated on the grid points and normalized over them, gives exactly the same table.

Bayesians have also skirted the intractable integrations by using algorithms like Markov Chain Monte Carlo (MCMC; see Meyer and Millar 1999) or sampling importance resampling (SIR; see McAllister and Ianelli 1997) to generate a random sample from the posterior distribution. Once such a sample is obtained, a histogram can be applied to represent the marginal posterior for each parameter. However, MCMC and SIR share a problem: they must converge or the answers are wrong (Gelman et al. 1995). In practice, this means running the algorithm for many hours (e.g., Hammond et al. 2001). Then the results must be subjected to a battery of convergence tests (SIR tests are not the same as MCMC ones), which requires the comprehension and presentation of some fairly intimidating diagnostics (e.g., Meyer and Millar 1999). Worse still, although these tests can reveal failed convergence, they cannot prove success (Cowles and Carlin 1996). As in classical hypothesis testing, the null hypothesis (that convergence has occurred) is never accepted: tests can only fail to reject it. If any test suggests convergence failure, then the run time must be extended, with no guarantee of success in finite time (Gelman et al. 1995).

Bayesian networks, by contrast, perform speedy, exact computations involving dozens of discrete random variables (DRVs) (Kuikka et al. 1999; Hammond and Ellis 2002). These networks are models of cause and effect that are always represented graphically (as in Fig. 1). In this representation, DRVs are depicted with labeled bubbles called nodes, and causal relationships are shown with arrows from cause to effect. In influence diagrams, a common extension of the Bayesian networks, the nodes can also include decision variables and utility functions (Oliver and Smith 1990). Each causal relationship is defined using a conditional probability table for the effect node, given the states of causal ones. Bayesian networks and influence diagrams allow a user to introduce evidence (i.e., data or observations) about the states of any nodes in the network and to propagate that evidence to others.

There are several algorithms for doing the propagation of evidence in Bayesian networks (Pearl 1988; Shenoy and Shafer 1990; Zhang and Poole 1996). The algorithm of Lauritzen and Spiegelhalter (1988), which is often referred to by the name of one of its data structures, the junction tree (also called the join tree in Pearl 1988), may be the most common at present. This algorithm focuses on graphical properties of the network and is quite complex in comparison with others. It may be popular because it efficiently computes the marginal probabilities for every variable in the network, not just for a given set of variables; though Cozman (2000) provides a method that achieves the same thing. A reader interested in the junction tree algorithm could consult a very readable textbook by Jensen (1996). All results in this paper were computed with it, which is not to say that other algorithms could not be substituted. This paper takes an object-oriented view of Bayesian networks, focusing on what they do, not on how they do it, a view afforded by readily available software (see below). For this reason, the paper will talk about generic Bayesian network propagation using the acronym BNP.

Thus, given a set of DRVs, $V = \{X_1, X_2, X_3, \ldots, X_k\}$, the purpose of a Bayesian network is to allow a user to introduce evidence about the states of any of the DRVs in V and to compute the resulting change in the marginal distribution of any of the others. For example, if the DRVs were all Boolean, a set of evidence E might consist of the information that X_1 = False, X_2 = True, and BNP could compute the probability that X_3 = True given this evidence.

Bayesian networks have already been used in a fisheries context (Kuikka et al. 1999; Hammond and Ellis 2002). In the work of Varis and Kuikka (1999), these networks have been used as meta-models for combining information from various sources, especially to support decision analysis. Varis and Kuikka (1997) used Bayesian networks to combine virtual population analysis (VPA) output with regression results to support the management of Baltic salmon. This combination was achieved using an approach called "uncertainty balance iteration", a method described more fully in Varis (1998). Though Varis and Kuikka (1997) associate stock assessment models and Bayesian networks, as will this paper, they do not do so with the aim of faithfully representing the model with the network. Instead, their aim was to add structural uncertainty to the VPA model in such a way that its predictions could be weighed against conflicting information from other sources. Thus, they ran the VPA model and the network in parallel layers. In Hammond and Ellis (2002), Bayesian networks were applied to parameter estimation in a fisheries context. Varis (1998) also discussed parameter estimation; however, a general approach to estimating parameters that would work on any hierarchical Bayesian model (given sufficient computer memory) has not been presented to date. This paper proposes one.

The aims of this paper are to describe a new approach to Bayesian analysis based on Bayesian networks, to illustrate it on a Schaefer assessment model, and to compare its answers both with those obtained by MCMC and with exact answers obtained by a combination of analytic computation and grid search (Walters and Ludwig 1994). The basic idea is to apply BNP to a stock assessment problem in a way that suggests how it might be applied elsewhere. To make BNP more generally applicable, a new technique called fuzzy discretization was created.

Methods

This paper provides a recipe for converting a hierarchical Bayesian model of continuous variables into a Bayesian network, using a process called fuzzy discretization. Once the model has been converted, BNP can be used to compute all

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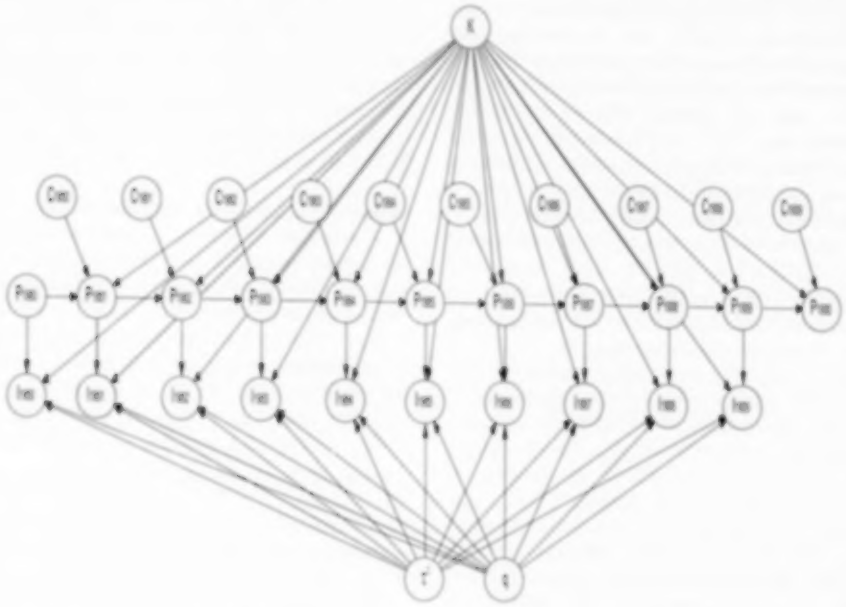
Fig. 1. This is a Bayesian network in which random variables are represented with labelled bubbles. Complete specification of this Bayesian network involves defining a conditional probability table for each variable. The table for a particular variable must be defined given the states of any other variables that point to it with arrows. For example, the table for P_{1981} would be conditional on P_{1980}, C_{1980}, and K.



marginal probabilities of interest. The key challenge is to make this conversion without significantly affecting estimation performance. This process is illustrated using a Schaefer stock assessment model. Naturally, an application of this recipe requires access to BNP software. Although a custom implementation of the algorithm in Lauritzen and Spiegelhalter (1988) was used to produce the results presented here (for reasons revealed below), results could also be produced with most of the Bayesian network software packages listed at http://www.ai.mit.edu/~murphyk/Bayes/bnsoft.html, some of which are free (look for ones that do inference by jtree, which is short for junction tree). To date, however, I have only tried HUGIN (www.hugin.com), because of familiarity rather than particular suitability. Detailed instructions for HUGIN implementation of this recipe are available from the author on request.

To apply BNP, Schaefer-model equations were first converted into conditional probability tables using fuzzy discretization. This new technique draws on ideas from fuzzy arithmetic (Ferson 1993) and is introduced in a separate section below. There follows a section on conditional distributions. Then this section gives the Schaefer model equations, data, and evaluation scenarios and ends with a description of the grid-search technique used for performance evaluation.

The WinBUGS code that was used to implement MCMC estimation is provided (Appendix A). WinBUGS is currently available free of charge from http://www.mrc-bsu.cam.ac.uk/bugs/welcome.shtml. In each evaluation scenario, MCMC ran for 500 000 iterations, after a burn-in of 20 000. Convergence was evaluated using the same diagnostics employed in Meyer and Millar (1999), namely Geweke's Z scores, Heidelberger and Welch's stationarity and half-width tests plus Raftery and Lewis' diagnostics (with the same specifications as in Meyer and Millar 1999), all of which are implemented in the free BOA software package (http://www.public-health.uiowa.edu/boa/).

Fuzzy discretization

Fuzzy discretization converts mathematical equations of continuous variables into discrete, conditional probability tables. Making such a conversion is useful because most models are specified with such equations, but Bayesian networks can only deal with tables. Fuzzy discretization, therefore, is what makes it possible to apply BNP to stock assessment.

Fuzzy discretization is not entirely new. Several key ideas were inspired by fuzzy arithmetic theory (Kaufmann and Gupta 1985) and bear a strong resemblance to concepts of that field. Differences could be considered primarily semantic. To acknowledge this debt, the "fuzzy" label has been retained in the new name. Also, the idea of discretizing continuous variables goes back so far that it would be difficult to correctly attribute an original source. Thus, the technique is best described as a new collection of old ideas. It will be introduced by representative examples.

Let us consider an example of fuzzy discretization using discrete numeric random variables called X, Y, and Z. Let X and Y have states {0, 1, 2, 3} and let Z have states {0, 2, 5}. The object is to obtain a conditional probability table for Z, namely $P(Z|X,Y)$, from the equation $Z = (X + Y)$.

For some cases it is relatively easy. When $X = 1$ and $Y = 1$, Z should be in state 2, as $1 + 1 = 2$. Therefore, fuzzy discretization would assign probability one to Z being in

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state 2 and probability zero to states 0 and 5. Similarly straightforward is $X = 0$, $Y = 0$, as Z should then be in state 0 with probability one.

For other cases, the "fuzzy result rule" applies. For example, when $X = 1$ and $Y = 2$, their sum is not a valid Z state. The two closest Z states are 2 and 5, and 3 is twice as far from 5 as it is from 2. Following this rule, fuzzy discretization would assign twice the probability to 2 that it assigns to 5 and other states would get nothing. When the exact answer falls between two states, the fuzzy result rule partitions all of the probability between them and the share assigned to each state is inversely proportional to the distance to the exact answer. If the exact answer falls outside the state grid, as it does when $X = 3$ and $Y = 3$, then all probability is assigned to the closest state, which would be 5.

In general, of course, equations can have any number of variables and may use all sorts of functions, but the principle is always the same. Compute the exact answer, compare it with the states of the result DRV, and apply the fuzzy result rule, as necessary. Some code is provided that can be useful in implementing fuzzy discretization in HUGIN and may serve to clarify a few implementation details, like the probability table format in that package (Appendix B). Implementation in other packages would be very similar.

Fuzzy discretization introduces error and the amount of error introduced is a function of the grid resolution of the result variable's numeric states. In the example above, if Z had been given states {0, 2, 3, 5}, the approximation entailed by the fuzzy result rule would have been improved. Thus, the application of fuzzy discretization should coincide with the use of fairly fine state grid resolution; the more states the better. The range of the grid is also important, and with a given number of grid states, there is a clear tradeoff between range and resolution.

Conditional distributions

Many statistical models specify parametric distributions for key random variables. Stock assessment models, for example, typically assign such parametric models to indices of abundance. Often, these parametric statistical models are described with "~" notation. In this notation, "K ~ Uniform(230, 340)" would declare that random variable K has a Uniform distribution over the interval from 230 to 340. Therefore, fuzzy discretization permits the construction of conditional probability tables from declarations in ~ notation.

Let DRVs X, Y, and Z be defined as above and consider the following declaration:

$$(1) \qquad Z \sim \text{Normal}((X + Y), Y)$$

from which we need to obtain the table $P(Z|X,Y)$. First, every pair of X and Y values would be associated with a Normal distribution. When $X = 1$ and $Y = 1$, for example, the distribution would be Normal(2,1), and this distribution would then be used to assign probability to the states of Z using the fuzzy distribution rule. Because Z has states {0, 2, 5}, the rule requires the computation of the grid midpoints {1, 3.5} (1 is half way between 0 and 2 and 3.5 is midway between 2 and 5). Then the rule would compute the probability that a Normal(2,1) random variable falls in each of three intervals: {(0, 1), (1, 3.5), (3.5, 5)}. Denoting these probabilities by $p1$, $p2$, and $p3$, respectively, and their sum by p_{tot}, the rule would assign probability $p1/p_{tot}$ to state 0, $p2/p_{tot}$ to state 2, and $p3/p_{tot}$ to state 5 (when $X = 1$ and $Y = 1$).

In fuzzy discretization, it is also useful to permit declarations in ~ notation for DRVs with interval states. Examples of such states include the numeric intervals (0, 3.5), (3.5, 8), and (8, ∞), wherein each state is understood to comprise all numbers between interval endpoints. This allows a user to specify the intervals directly, rather than having them computed from grid midpoints, but is otherwise very similar.

Schaefer model data and equations

For testing purposes, 10 years worth of landings and survey catch-per-unit-effort (CPUE) data were simulated (Table 1). Simulated population dynamics followed Schaefer-model assumptions with $r = 0.29$, $q = 0.2$, and $K = 280$ (see below for parameter definitions). The variant of the Schaefer model found in Meyer and Millar (1999) was used. The equation is as follows:

$$(2) \qquad P_{t+1} = P_t + rP_t(1 - P_t) - C_t/K$$

In eq. 2, K is the carrying capacity, r is the population growth rate, P_t is the biomass divided by K in year t, and C_t is the catch in that year (Table 1). In both simulation and estimation, the population was started at the carrying capacity K in 1980. In other words, $P_{1980} = 1$.

The model for the survey CPUE data (Table 1) (denoted I_t) is defined in the following declaration:

$$(3) \qquad I_t \sim \text{Lognormal}(\log(qP_tK), \tau^2)$$

where q is the survey catchability coefficient and τ^2 is the Lognormal dispersion parameter. The Lognormal distribution is parameterized here by the mean and variance of the associated Normal distribution. Realizations of the survey CPUE index random variables are here denoted by i_t.

This being a Bayesian model, priors were needed as well. For convenient comparison to analytic results using equations in Walters and Ludwig (1994), r was set equal to 0.29, which could be described as a very sharp prior. As in that paper, noninformative priors were assigned to q and τ^2; these were proportional to $1/q$ and $1/\tau^2$, respectively. A flat improper prior was assigned to K.

Grid search with analytic integration

Three different estimation scenarios were used to evaluate the performance of BNP. In the first, $q = 0.2$ and $\tau^2 = 0.012$; in the second, q was estimated but $\tau^2 = 0.012$; and in the third, q and τ^2 were both estimated. Parameter K was estimated in all three. These scenarios were selected because they lend themselves to "exact" computation of results via grid search by analytically integrating out parameters q and τ^2 (when they were not fixed). In fact, equations for assigning relative probability levels to different values of parameter K under each scenario are derived in Walters and Ludwig (1994). Results are "exact' in the sense described in the Introduction because only one parameter remains once the nuisance parameters q and τ^2 are integrated out analytically.

To reproduce the equations of Walters and Ludwig (1994) here, let us define the $n = 10$ statistics $Z_t = \log(i_t) - \log(P_t) -$

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Table 1. The simulated catch in tonnes (t) and survey catch-per-unit-effort (CPUE) data used in computing all results.

Year	Catch (t)	Survey CPUE ($kg \cdot h^{-1}$)
1980	21.68	60.23
1981	34.12	48.06
1982	46.51	47.46
1983	41.26	40.45
1984	42.87	40.07
1985	36.62	32.99
1986	26.11	26.64
1987	24.93	25.44
1988	21.48	24.13
1989	21.97	24.68

$\log(K)$ for $t = 1980$ to 1989, and let us denote their mean by $\bar{Z}$ and their sample variance by S^2. Then, in scenario 1, the likelihood kernel for assigning relative probability to the grid points of K is given by the following equation:

$$(4) \qquad L_1 = \tau^{-n}\exp[-[(n-1)S^2 + n(\log(q) - \bar{Z})^2]/(2\tau^2)]$$

Though no K appears explicitly in eq. 4, the two statistics S^2 and $\bar{Z}$ are functions of K. In scenario 2, relative probability levels can be assigned by

$$(5) \qquad L_2 = \tau^{-n/2}\exp[-(n-1)S^2/(2\tau^2)]$$

In scenario 3, the likelihood kernel simplifies to

$$(6) \qquad L_3 = (S^2)^{-(n-1)/2}$$

To recap, eqs. 4 to 6 are "exact" in the sense that, for any grid point g of K, the analytic – grid search probability associated with g from these equations (denoted $p_{GS}(g)$), is proportional to the true marginal posterior density for K (p_K) evaluated at g. In other words, $p_{GS}(g) \propto p_K(g)$. Moreover, if the $p_K(g)$ were normalized to sum to 1 over the grid states of K, they must be exactly equal to $p_{GS}(g)$.

Grid selection

Then the only task remaining was to select a grid of states for K. The main problem, in any application of grid search, is to make the grid of parameter values match the region of high marginal posterior probability, a job usually accomplished by trial and error. A good strategy for grid selection is to start with a broad grid and then to zoom in gradually on regions of high posterior probability. Examine the marginal distribution of each variable at each step to help in grid refinement.

I illustrate four possibilities that can result from viewing the same marginal posterior probability table with different grids, all of which have 25 states (Fig. 2). One possibility provides a template for the type of marginal posterior to aim for (Fig. 2*a*). This ideal result devotes exactly two grid points to delimiting the support of the distribution, saving all others for depicting the distribution's shape. Initial attempts with broad grids will tend to waste grid points by storing too many zeros (Fig. 2*b*). Zoom in such grids. The two remaining possibilities may indicate problems (Figs. 2*c* and 2*d*). In almost all cases, if the marginal distribution for any variable looks "cut off" at one end, as in these panels, all results should be regarded with prejudice (bias can be considerable) until the grid is extended in the appropriate direction. It might be acceptable, however, for a positive variable to appear cut off at zero. Other scenarios could probably be cooked up, where marginal probability is legitimately positive at grid endpoints, but such scenarios are exceptional in practice. As a rule of thumb, be suspicious of truncated marginal distributions (Figs. 2*c* and 2*d*) unless these can be explained. Beware of multiple modes in the distributions; only broad initial grids can pick these up.

By trial and error, a uniform grid of 30 states extending from 240 to 330 tons was chosen for K. The same grid was used in all three scenarios to facilitate comparison.

Implementation with Bayesian networks

A visual representation of our Schaefer model is provided (Fig. 1) and indicates what to expect in this section. Subsequent paragraphs describe how to attach a probability table to each of the DRVs represented by bubble nodes (Fig. 1), except for the catch values, C_t (from Table 1). As soon as every node has a table, BNP can propagate evidence about the state of network DRVs around the network. The recipe will reveal where this evidence entered the network and what it was. For comparison to grid search, the Bayesian network computed the marginal posterior for K under each of the three scenarios.

As in grid search, this recipe requires the selection of parameter value grids. As in that approach, these grids must be selected by trial and error, using exactly the same procedure described above. To make comparison to grid search easier, however, parameter K was given the state grid used above. State grids must also be assigned to q and τ^2 in scenarios where they are not constant. Both were given 25 states, uniformly distributed in log space. Furthermore, grids must be given to all population state DRVs P_t, for $t = 1981$ up to 1990 (recall that $P_{1980} = 1$). Initially, these variables were given 35 states spaced evenly from 0.001 to 1, but subsequently, these grids were zoomed in on high probability regions of the population trajectory to cut down on fuzzy discretization error. Thus this recipe is very much an iterative process of grid refinement.

The next step is to produce probability tables. To this end, fuzzy discretization was applied to eq. 2, after substituting 0.29 for r, yielding tables $P(P_{t+1}|K, C_t, P_t)$ for $t = 1980$ to 1989. In making the unconditional table for K, equal probability was assigned to each state to be consistent with the prior. Tables for q and τ^2 were needed too for the scenarios where they were not constant. As the states for these parameters were uniform in log space, each state got equal probability, as suggested by the priors (because q must have density proportional to $1/q$ if $\log(q)$ has a uniform distribution). Probability tables were then given to the index variables using a technique that introduces another source of approximation error.

The trick with the indices, I_t for $t = 1980$ to 1989 is to model them with interval DRVs. Each index variable I_t was given the following three interval states: $[(0, 0.999i_t), (0.999i_t, 1.001i_t), (1.001i_t, \infty)]$, where i_t is the observed CPUE

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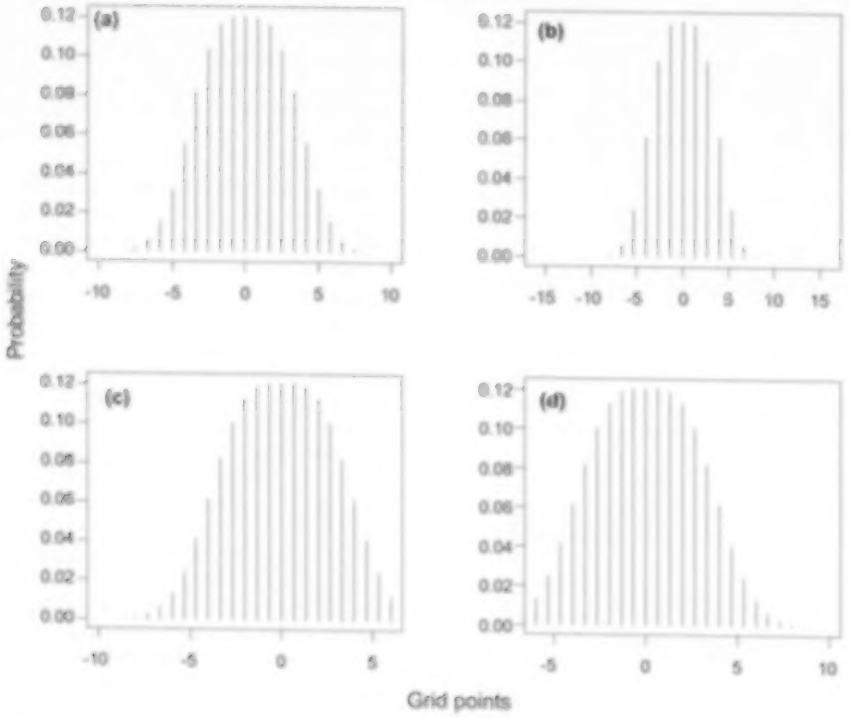
Fig. 2. This sequence of panels shows the same continuous marginal distribution, as viewed using a selection of discrete grids, all of which have 25 states. The vertical lines in each panel indicate the relative probabilities assigned to each grid point. (*a*) The ideal grid selection, with one grid point on each end showing zero probability, to delimit the distribution's support. (*b*) The loss of detail entailed by a grid that is too broad. (*c* and *d*) Grids that are cut off in the right and left tails, respectively. Those two grids must be extended to cover the distribution's entire support; otherwise results could be severely biased.



value in year t (Table 1). For simplicity, these states were relabeled "under", "near", and "over" the observed value, respectively. Because fuzzy discretization understands declarations like eq. 3 for interval DRVs, it was used to create conditional distributions for all index variables. Admittedly, multiplying the observed index value by 0.999 or by 1.001 in this way introduces a bit of approximation error; however, changing these multipliers to 0.9999 and 1.0001 had practically no effect on results.

To explain what this trick is doing, it will be necessary to introduce a bit of notation. In a more typical stock assessment, the contribution of each index value i_t to the likelihood function for parameter set θ is a factor given by the density function for the index, evaluated at i_t (in other words, by $f_{I_t}(i_t|\theta)$). The product of these factors over all of the years forms the likelihood function, $l(\theta)$, which is normally used to weigh the evidence for and against contending parameter vectors (with the prior, in the Bayesian case, and with other likelihood components, in more complex assessments). Now factors that do not depend on θ can be dropped from the likelihood function without affecting the weight assigned to contending model parameterizations (as this merely corresponds to changing units of weight). Remembering that, let us pose the question: what if, in place of the density function, $f_{I_t}(i_t|\theta)$, we substituted the probability that the index variable lies "near" the observed value, where "near" means in the interval $((1 - \triangle)i_t, (1 + \triangle)i_t)$, for some small $\triangle$ (like the 0.001 used above)? How much error would be made in weighing evidence like that?

Qualitatively speaking, the answer is "not much". To see this, first note that the probability that the index value lies "near" i_t would be calculated using the distribution function: it would be $F_{I_t}((1 + \triangle)i_t|\theta) - F_{I_t}((1 - \triangle)i_t|\theta)$. Second, because this "weight" can be safely multiplied by a factor independent of θ, let us divide it by $2\triangle i_t$. The resulting quotient is the rise in the distribution function over the interval $((1 - \triangle)i_t, (1 + \triangle)i_t)$, divided by the interval length. The limit of this quotient, as $\triangle$ tends to 0, is the derivative of the distribution function at i_t, in other word $f_{I_t}(i_t|\theta)$, the very thing we want. So, as $\triangle$ gets smaller, the approximation to normal inference improves.

As in any Bayesian network application, the last stage is to introduce evidence and to propagate it around the network. The evidence introduced was that each I_t variable was "near" the observed level. In other words, I_t was given interval state $(0.999i_t, 1.001i_t)$, for all t from 1980 to 1989. This done, BNP propagated the evidence and computed the marginal probability for each state of K under each scenario.

Results

The marginal posterior results for K produced by BNP and MCMC in scenario 1 are displayed alongside the exact results from grid search (Fig. 3). Although the BNP result

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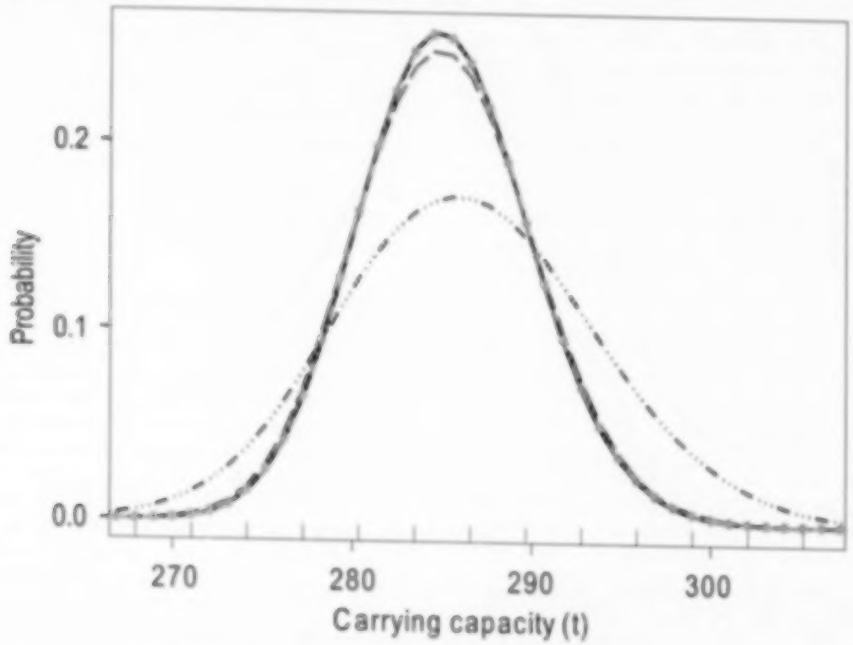
Fig. 3. The marginal posterior density estimates for K from Bayesian Network Propagation (BNP) and Markov Chain Monte Carlo (MCMC) are compared with the "exact" answer for scenario 1, where only parameter K was estimated. The "exact" result (solid line) and the BNP estimate (shaded line of dots and dashes with circles) are virtually indistinguishable by eye, but the MCMC estimate (dark broken line) falls a bit below. The grid of K states used throughout the paper is shown with a rug of tick marks along the horizontal axis. Note that the "exact" answer is really only exact on these grid points, as stated in the main text. The initial BNP density estimate obtained before zooming the P grids in on regions of high posterior probability is also shown (line with 3 dots between dashes), illustrating the dramatic performance improvement this entails.



was virtually indistinguishable from the exact answer, MCMC showed discernible error. One index of this error is obtained by the sum of squared differences over the grid points of K, here referred to as sum square error (SSE). For BNP, the SSE was 3.4×10^{-6}, but for MCMC, it was 2.0×10^{-4}. The figure also shows the rather poor initial BNP estimate, obtained before zooming the population state (P) grids onto intervals of high posterior probability.

In scenario 2, the BNP SSE was 7.9×10^{-6} to MCMCs 5.3×10^{-5} (Fig. 4), whereas in scenario 3, the BNP SSE was 1.5×10^{-4} and the MCMC SSE was 4.4×10^{-4} (Fig. 5). In the last scenario, an MCMC density estimate obtained with only 250 000 iterations was visually indistinguishable from the full-chain results (Fig. 5), suggesting that the rate of improvement is slow. None of the three MCMC convergence diagnostics used in Meyer and Millar (1999) reported any convergence problems in any scenario, even when the chain length was reduced to 250 000 (as in that paper). The reduced chains produced SSE results of 2.0×10^{-4}, 6.3×10^{-5}, and 4.5×10^{-4} in the three scenarios, respectively.

The run time for BNP, for a given set of grids, was 3 s in scenario 1, 3 min in scenario 2, and 67 min in scenario 3. Scenario 3 was dramatically slower because the computer was using virtual memory. Running the scenario 3 program with only 25 states for the population states, P_t for t = 1981 to 1990, instead of 35 states, yielded results in 20 min. For MCMC, the run times were 6 h 10 min, 6 h 20 min, and 6 h 49 min for scenarios 1 to 3, respectively, on the same computer.

Discussion

This paper describes a new approach to Bayesian analysis based on BNP by giving an example of its application to a Schaefer stock-assessment problem. The main advantage of this new approach is that it does not have to converge in the way that MCMC (the most common Bayesian algorithm) does. In other words, MCMC convergence evaluation tools like Geweke's Z scores, Heidelberger and Welch's stationarity and half-width tests, and Raftery and Lewis' convergence diagnostics (cf. Cowles and Carlin 1996) would not be needed.

Dispensing with convergence diagnostics by using fuzzy discretization and BNP introduces two sources of approximation error: one from assigning continuous function results to DRVs, and another from approximating the likelihood of a continuous data point (e.g., a survey index) with the probability that it was "near" the observed value. This paper demonstrates, however, that resulting errors in density estimates can be smaller than those resulting from imperfect MCMC convergence, even when standard convergence diagnostics report no problems. On the fisheries-related scenarios studied in this paper, BNP outperformed the standard approach, both in speed and accuracy.

The BNP recipe has much in common with grid search. As in that method, it requires the user to select discrete grids of parameter states and to refine these grids by trial and error. In both methods, the process of grid refinement (suggested above) would lend itself to computer automation. The

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Fig. 4. The marginal posterior density estimates for K from Bayesian Network Propagation (BNP, shaded dotted and dashed line) and Markov Chain Monte Carlo (MCMC, broken line) are compared with the "exact" answer (solid line) for scenario 2, in which parameters K and q were estimated. BNP outperforms MCMC. The K state grid is shown with a rug of tick marks along the horizontal axis. Recall that the "exact" answer is really only exact on these tick marks; density values between these marks were obtained by cubic-spline interpolation.

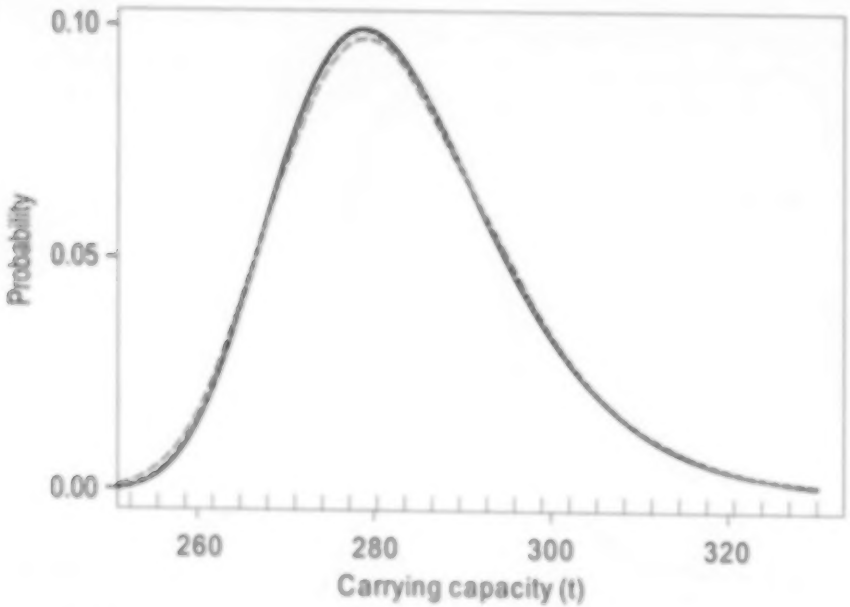
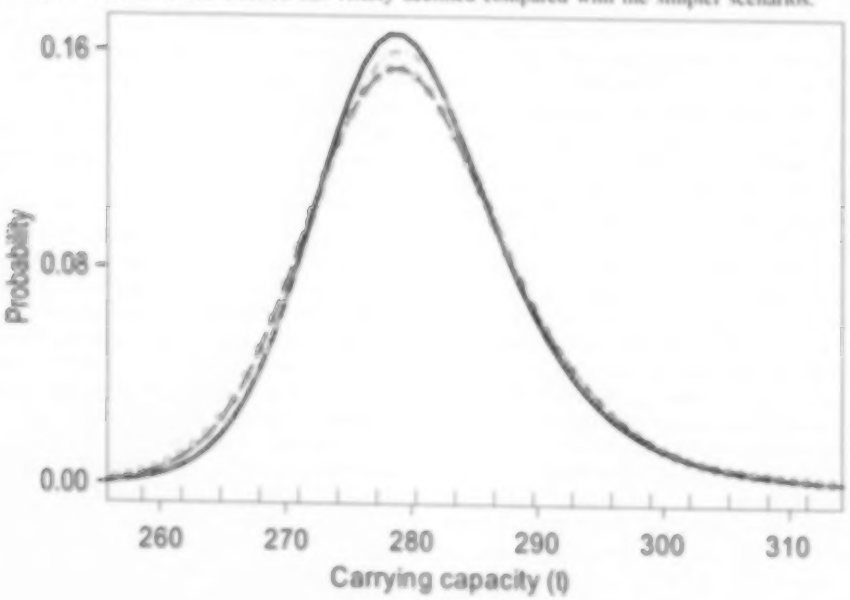


Fig. 5. The marginal posterior density estimates for K from Bayesian Network Propagation (BNP, shaded dotted and dashed line) and Markov Chain Monte Carlo (MCMC, broken line) are compared with the "exact" answer (solid line) for scenario 3, in which parameters K, q, and τ^2 were all estimated. BNP outperforms MCMC once again. MCMC results obtained with only 250 000 iterations (as opposed to 500 000) are also indicated (two dots between circles). These short-run results are virtually indistinguishable from the long-run ones. The performance of both BNP and MCMC has visibly declined compared with the simpler scenarios.



refinement process makes parameter grids converge onto the region of high marginal posterior probability. Although this sort of convergence is different from the sort required in MCMC, it could also fail. Such failure seems unlikely, however, because the convergence process is more understandable than MCMCs, with clearer stopping criteria. This

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recipe also shares a weakness of grid search: difficulty in dealing with highly correlated parameters, though it cannot be said that MCMC has an easy time with them. Basically, key portions of the posterior can slip through the state grids. Walters and Ludwig (1994) give a discussion of this problem with reference to the Schaefer model, along with a few suggestions on how to deal with it (use lots of grid points, zoom in, and reparameterize). Though these suggestions apply equally well to the BNP approach, the method is not foolproof.

A key difference between the BNP approach and grid search is that the latter uses the joint posterior function to weigh the evidence for and against different model parameterizations, as described in the Introduction (or a likelihood kernel, as in eqs. 4 to 6), whereas the former does not. Converting the model to a Bayesian network allows BNP to do all of the estimation work; like WinBUGS, it never needs to be told the full joint posterior.

Although grid search will outperform BNP when both are applicable, the latter is useful because grid search cannot process large numbers of parameters. Grid search does well with one or two parameters, can handle up to about seven, but anything much beyond that is unrealistic because of computer memory constraints (at 25 states per variable, the joint probability table for seven variables would need more than six billion entries). BNP, on the other hand, has been shown to work on Bayesian networks with dozens of DRVs, so it is far more general in its potential applicability. Where grid search is applicable, however, it should be used in preference to BNP or MCMC.

To understand how Bayesian networks can handle dozens of DRVs when grid search would flounder, it is important to distinguish two types of model complexity: global and local. Global complexity refers simply to the total number of DRVs in the model. Local complexity, on the other hand, must be understood with reference to the graphical representation of the model. Local complexity is maximum number of incoming arrows to network nodes. The index variables (I_t) have four incoming arrows in the current model, implying that the conditional probability table required for these nodes is larger than the one required for the populations states (P_t).

Computer memory constraints limit the global complexity of models to which grid search can be applied. An important attraction of Bayesian networks, however, is that they tend to be limited more by the local than by the global complexity (though the latter is not irrelevant). The number of states assigned to each variable is also important. Generally, the more locally simple the Bayesian network, the more globally complex it can grow, yet still fit in computer memory. Incidentally, having a lot of outgoing arrows from a particular variable, as with K in the current model, is of no concern. Process error models, like the one in Meyer and Millar (1999), should tend to be suitable to a BNP implementation because they would add little or no local complexity to the graphical representation, while adding lots of the global sort.

Thus, a reader wanting to gauge whether a particular model is amenable to the sort of Bayesian network implementation suggested in this paper should draw its graphical representation. As a very rough rule of thumb, for networks with about 25 states per variable, if there are more than about five incoming links to any particular node, today's personal computers are probably going to choke (unless the model is globally simple). That having been said, adding intermediate variables can often reduce the local complexity of a given model. In some age-structured assessment models, for example, the spawning stock biomass (SSB) is obtained by a weighted sum over the numbers-at-age in each year. So, if there were more than five age classes, the rule of thumb might seem to preclude Bayesian network implementation, as SSB would have more than five incoming arrows. Such is not the case, however, because intermediate variables can be added to the model to hold partial sums. One intermediate variable could hold the weighted sum of the first four age classes; another could hold the next four and so on. SSB could then be defined as the sum of these added partial sums, removing the local complexity problem. It should be noted, however, that fuzzy discretization would exact a small performance toll for every intermediate variable added in this way because of the fuzzy result rule.

Therefore, while fuzzy discretization can convert any hierarchical Bayesian model to a Bayesian network, not all resulting networks can be held in the computer memory. If they cannot be held in the memory, BNP will not work. There are certainly some multispecies, size-structured, spatial models with migration that could not be implemented with this recipe. MCMC, on the other hand, could attempt these highly parameterized problems, though the accuracy of the solution would be unclear. Further research is required to ensure that the diagnostic tools correctly identify convergence failure. The fact that MCMC will let a scientist take on an impossibly complex problem, while BNP will not, is not necessarily a point in MCMC's favor. There is a lot to be said for sticking to simple models, at least to locally simple ones.

In closing, let us briefly consider an analogy between this estimation recipe and the sonic hunting strategy of dolphins and bats. The noises that these animals emit in searching for their prey are a bit like the grid points required in this approach. Recordings of these sounds, processed to be audible to human ears, suggest that these animals increase the chirp and click rate as they home in on their prey. Their behavior suggests a conjecture: rather than using a uniform grid, as applied to K in this paper, might it not be more efficient to tighten the grid resolution near the posterior mode by sacrificing resolution in the tails? For a fixed number of grid points, doing so ought to improve estimation performance, if only because foraging behavior tends to be optimized.

Acknowledgments

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Appendix A

The following code allows implementation of scenario 3 estimation using WinBUGS.

```
model surplusproduction;
var C[10], I[10],Imed[10],P[10],r,K,q,iq,itau2,P1990;
{
K~dunif(220,340);
r<-.29;
iq~dgamma(0.00001, 0.00001)I(0.5,100);
q<-1/iq;
itau2~dgamma(0.00001, 0.00001)
P[1]<-1;
for (t in 2:10) {
P[t]<-P[t-1]+r*P[t-1]*(1-P[t-1])-C[t-1]/K;
}
for (t in 1:10) {
Imed[t]<-log(q*K*P[t]);
I[t]~dlnorm(Imed[t],itau2);
}
P1990<-P[10]+r*P[10]*(1-P[10])-C[10]/K;
}
```

Data

```
list(C=c(21.68,34.12,46.51,41.26,42.87,36.62,26.11,24.93,21.48,
21.97),
I=c(60.23, 48.06, 47.46, 40.45, 40.07, 32.99, 26.64, 25.44, 24.13,
24.68))
```

Inputs

```
list(K=240, iq=40, itau2=15)
```

Scenario 2 can be implemented by changing the inputs to `list(K=240, iq=4)` and by changing `itau2~dgamma(0.00001, 0.00001)` to `itau2<-1/0.012` in the model code. Scenario 1 can be implemented by further changing the inputs to `list(K=240)` and by substituting `q<-0.2` for both `iq~dgamma(0.00001, 0.00001)` and `q<-1/iq;`.

The MCMC results in Figs. 2 to 4 were produced by applying kernel density estimation to the CODA output from WinBUGS for parameter *K*.

Appendix B

This appendix provides *R* functions that clarify, generalize, and facilitate the task of generating probability tables from equations. Novice users of this freely available language (http://www.r-project.org/) need only paste the code onto the command line from a text editor. This appendix also assumes that the reader has access to the freeware version of HUGIN (called HUGIN Lite, available at www.hugin.com) in order to make more specific, hands-on recommendations and to avert some of the confusion that tends to surround new methods.

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The first *R* function, fuzzy.interpolate, takes as arguments a function result (x) and a vector of grid values (grid) onto which the function results are to be interpolated. It returns a vector of probabilities over the states in grid, as specified by the "fuzzy result rule".

```
fuzzy.interpolate<-function(x, grid) {
  n<-length(grid)
  ans<-rep(0,n)
  test<-grid[grid >= x]
  if (length(test) = = 0) {
  ans[n]<-1
  return (ans)
  }
  if (length(test) = = n) {
  ans[1]<-1
  return (ans)
  }
  #Set i to the first index in grid where the entry is bigger than or
    equal to x
  i<-match(test[1], grid)
  denom<-grid[i]-grid[i-1]
  p1<-(x-grid[i-1])/denom
  ans[i]<-p1
  ans[i-1]<-1-p1
  return(ans)
  }
```

The second function, fuzzy.vect, takes a whole vector of function results (x) and a vector of grid values (grid). It returns a probability table, represented as a matrix, with rows corresponding to the entries in grid and columns corresponding to the entries of x.

```
fuzzy.vect<-function(x, grid) {
m<-length(x)
n<-length(grid)
ans<-matrix(0, n, m)
for (i in (1:m)) {
ans[,i]<-fuzzy.interpolate(x[i],grid)
}
return(ans)
}
```

The use of these functions is illustrated by returning to the example of obtaining $P(Z|X,Y)$ from equation $Z = X + Y$, assuming states {0,1,2,3} for X and Y and {0,2,5} for Z, as discussed in the main text. Let us assume that "Numbered" nodes (with numeric states) for the three variables have been created in HUGIN (with the discrete chance tool), that edges have been added from X to Z and also from Y to Z (with the link tool), and that each variable has been given the appropriate states.

Now, the Produce.Z.table function, below, can be used to compute the desired table:

```
Produce.Z.table<-function () {
  Zstates<-c(0,2,5)
  Xstates<-0:3
  Ystates<-0:3
  z<-kronecker(Xstates, Ystates, FUN="+")
  ans<-fuzzy.vect(z,Zstates)
  write.table(ans, file="Ztab.csv", sep=",", quot=F, row.names=F,
    col.names=F)
  return(ans)
  }
```

It uses "kronecker", a standard *R* routine that applies the bivariate function specified by "FUN" to every combination of entries in X and Y, returning the result as a vector. Our new *R* function can be invoked with the command "Produce.Z.table()". It writes the table to a file called "Ztab.csv", the contents of which are suitable for pasting directly into HUGIN's probability table editor, provided the file is first opened with a spreadsheet like Microsoft EXCEL®.

Any Bayesian Network program will provide a similar means of entering probability tables onto network nodes. The results in this paper, however, were produced by generating the conditional probability tables directly with custom BNP software. This saves the need to import tables and thus speeds up the application considerably. Therefore, the best packages for implementation of this recipe are ones that provide an application program interface (API), a means of interacting with Bayesian networks in your own programs. HUGIN Developer® already provides such a thing, though it is not cheap. The Netica API (www.norsys.com) is another possibility. With such software, there would be no need for the tedious cutting and pasting described above.

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Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery

Eric A. Parkinson, John R. Post, and Sean P. Cox

Abstract: A freshwater sport fishery that targets hundreds of geographically isolated stocks is simulated by combining a model of angler behavior with a model of rainbow trout (*Oncorhynchus mykiss*) population dynamics. Ideal free distribution (IFD) theory, which suggests that angling quality will be similar on all lakes, is used to drive angler effort distribution. Model parameters are based on creel survey data from 53 lakes and empirical relationships between growth, survival, and density derived from whole-lake density manipulations on nine lakes over a period of 10 years. We compared angling quality, population density, fish size, and yield under unfished conditions, harvest rates that maximize sustained yields (MSY), and an IFD equilibrium driven by angler behavior. The IFD equilibrium rarely maximized yields. Stocks with high MSY angling quality are overexploited at the IFD equilibrium because anglers move to take advantage of exceptional angling opportunities. These stocks would often be viewed as more resistant to harvest pressure because they have higher stock productivities and habitat capacities. However, in our model, they are systematically overharvested because their high fish density attracts excessive angling pressure. Conversely, stocks with low MSY angling quality are underexploited because anglers move to take advantage of better angling quality on other lakes.

Résumé : La combinaison d'un modèle de comportement des pêcheurs à un modèle de dynamique de population de la truite arc-en-ciel (*Oncorhynchus mykiss*) nous a permis de simuler une pêche sportive d'eau douce qui cible des centaines de stocks isolés géographiquement. La distribution libre idéale (IFD), qui suppose que la qualité de la pêche sera la même dans tous les lacs, détermine la répartition des efforts de pêche des pêcheurs. Les variables du modèles sont tirées de statistiques de pêche sportive dans 53 lacs et les relations empiriques entre la croissance, la densité et la survie ont été obtenues par des manipulations de la densité dans neuf lacs entiers sur une période de 10 ans. Nous avons comparé la qualité de la pêche, la densité de la population, la taille des poissons et le rendement de la pêche en l'absence de pêche sportive, ainsi qu'à des taux de récolte qui maximisent le rendement soutenable (MSY) et à un équilibre IFD dû au comportement des pêcheurs. Les stocks avec une qualité de pêche de fort MSY sont surexploités à l'équilibre IFD, car les pêcheurs se déplacent pour jouir des conditions exceptionnelles de pêche. Ces stocks seraient souvent considérés comme plus résistants à la pression de capture parce qu'ils ont une plus forte productivité et font une utilisation plus grande de l'habitat. Cependant, dans notre modèle, ces stocks sont systématiquement surexploités, parce que leurs fortes densités de poissons suscitent une pression de pêche excessive. Inversement, les stocks qui possèdent une qualité de pêche de faible MSY sont sous-exploités, car les pêcheurs se déplacent vers d'autres lacs pour profiter des meilleures conditions de pêche.

[Traduit par la Rédaction]

Introduction

A fundamental problem in managing multistock fisheries is that optimal harvest rates often vary substantially among stocks because of variation in stock–recruitment parameters. When multiple stocks are harvested at a single place and time, this variation in optimal harvest rates implies that the maximum yield of the mixed-stock fishery will be less than the combined maximum yields of the individual stocks (Paulik et al. 1967). If fishers can target individual stocks, the problem of multistock management is substantially reduced and, in theory, maximum yields can be achieved for each stock. In reality, fishery managers rarely have tight control over either the total effort or the allocation of har-

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vesting effort among individually targeted stocks. This raises the possibility that some stocks will be overharvested, even if total effort in the fishery is not excessive.

The two main approaches to the problem of overexploitation have been the biological theory of stock–recruitment relationships (Ricker 1975) and the economic theory of exploitation of a common property resource (Gordon 1954). In general terms, the biological theory of population regulation suggests that there are optimum population levels that will achieve the desired balance between the conflicting goals of maximizing yield or economic value while minimizing risk of collapse (Hilborn and Walters 1992). In sport fisheries, maximum sustainable biomass yields can be replaced by a maximum sustainable benefit, which can be defined as angler effort multiplied by a measure of angling quality. Quantitative models of recruitment dynamics and yield range from simple two-parameter analytic models (Barrowman and Myers 2000) to complex age-structured models (Peterson and Evans 2003; Post et al. 2003).

Economic theory predicts that exploitation will be driven by fishers' expectations of economic returns. The distribution of effort will be determined by the relative economic returns in alternative fisheries (Holland and Sutinen 1999). For commercial fisheries with open access (i.e., effort is not restricted), many authors have recognized that economic forces, poor data, and lack of catch restrictions often result in the severe overharvest of many common property resources (Hilborn 1985; Ludwig et al. 1993). In simple terms, an economic equilibrium results when boats stop entering a fishery because exploitation has driven catch per unit effort (CPUE) down to the point where revenue from sales is equal to the cost of fishing. In many cases, this equilibrium results in excessive fishing effort and depressed fished populations, which, in turn, result in various schemes designed to reduce effort (DeVoretz and Schwindt 1985). The equivalent of an economic equilibrium in a sport fishery occurs when harvest by anglers drives angling quality down to the point where additional anglers stop entering the fishery.

Freshwater sport fisheries are often based on many small, independent population units (stocks in hundreds of lakes) that are tied together into a single fishery by a mobile angling population (Billings 1989; Shuter et al. 1998). In multilake systems, angler movement among lakes is an important factor driving changes in angling quality. The movement behavior of anglers can be modeled using ideal free distribution (IFD) theory, which has been developed by behavioral ecologists to predict the distribution of foragers relative to the distribution of their prey resources (e.g., Gillis et al. 1993; Levin et al. 2000). IFD theory predicts that angling quality should be similar on all lakes. This prediction is based on the belief that differences in angling quality should result in shifts in effort that, at equilibrium, result in a situation where individual anglers cannot experience an improvement in quality by moving to another lake (Cox et al. 2002). Assumptions in IFD theory include zero cost to moving, perfect information about angling quality on all lakes, equivalent costs (e.g., travel time, regulation complexity) on all lakes, and equivalent ancillary benefits (e.g., facilities, aesthetics) on all lakes. In the simplest case, when fish size is not included in either the biological and harvest models, IFD theory suggests that numbers caught per unit of effort (NPUE) should be the same on all lakes (Cox 2000; Post et al. 2002). However, size structure is clearly an important factor in both angling quality and the dynamics of fish populations. Angling quality can be defined in terms of individual fish size and the total weight of the catch in addition to the number of fish caught. However, various combinations of fish size and NPUE can be defined as equivalent if it can be shown that anglers do not prefer one combination over another (e.g., many small fish versus fewer large fish). External factors, such as aesthetics and facilities, also influence angling quality but are usually assumed to be independent of fish population structure.

In contrast with the homogeneity in angling quality predicted by IFD theory, observations of fish habitat and populations suggest that optimal densities will vary among lakes. For example, the rainbow trout (*Oncorhynchus mykiss*) fishery on the interior plateau of British Columbia, Canada, is supported by many small, independent stocks that vary substantially in both density and size structure. This variation among lakes can be linked to variation in the quality and quantity of stream spawning areas (Larkin 1954) and lake habitat (Northcote and Larkin 1956), which suggests that optimal densities and harvest rates should also differ among lakes. The contrast between variation in optimal densities and the homogeneity predicted by IFD theory implies that the dynamics of the angler effort response will rarely result in optimal harvest rates in fisheries where effort is free to move among biologically independent populations. This contrast reflects the situation for many single-stock fisheries where the economic equilibrium typically does not match the optimum derived from stock–recruitment theory.

In this paper, we explore the dynamic interactions between angler effort and fish populations that vary in biological productivity and examine the implications in terms of harvest. Our goal is to identify conditions that are likely lead to overexploitation in open access fisheries and quantify the gains that might be expected under alternative management policies. We explore these interactions in two stages. First, we develop a simple analytical model to illustrate the general problem. Second, we develop a more complex size-structured simulation model that directly links angling quality (catch rates and fish size) data to angler behavior, biological productivity, and harvest outcomes. We develop and parameterize this simulation model with biological and fishery processes and data from Walters and Post (1993), Post et al. (1999), Cox (2000), and Post et al. (2002).

Methods

Model development and parameterization

Our simulations model a fishery that consists of multiple stocks that are biologically independent but are exploited by a common pool of harvesting effort. Two population models drive the dynamics of fish growth, survival, and reproduction. A simple numerical model is used to illustrate the general behavior of this type of system. A size-structured model provides a more accurate depiction of the demographic and harvest processes that are both strongly size dependent. Model parameters are derived from monoculture, lacustrine rainbow trout populations in British Columbia Management Region 3. In both models, biological differences among pop-

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ulations are simulated by varying the maximum rate of increase at low population density (stock productivity) and the maximum population density over a plausible range for monoculture rainbow trout in British Columbia lakes. Angling quality is linked to the fish population model using empirical catchability data. To simulate the effects of mobile effort, we used the IFD prediction that angling quality will be similar on all stocks. The IFD equilibrium is driven by effort that moves among lakes when angling quality is either better (more anglers go to a lake) or worse (some anglers leave) than the average in Region 3. The IFD equilibrium is found by searching for an effort level that produces both the target angling quality and a stable fish population. The same models were used to evaluate the status of the fishery under both minimal and optimal harvest rates. Optimal conditions for each fish population are those that maximize yield.

A simple numerical model

Recruitment was modeled with a Beverton–Holt stock–recruitment relationship between the lake density (fish per hectare) of spawners (N) and recruits (N_t).

$$(1) \qquad N_t = \frac{\alpha N}{(1 + \alpha N/\beta)}$$

The demographic parameters of the fish population are stock productivity (α is the maximum recruits per spawner) and habitat capacity (β is the asymptotic density of progeny produced with very large spawner densities). Parameters were varied over an eightfold range in the case of β (50, 100, 200, and 400 fish·ha^{-1}; Stringer et al. 1980) and a fourfold range for α (2, 4, 8, and recruits·spawner^{-1}; Myers et al. 1999).

With the addition of catchability (q), harvest mortality can be incorporated into eq. 1. If angling effort (E, angler-days per hectare) is constant, harvest rate (HR) is a density-independent function of q and E.

$$(2) \qquad \mathrm{HR} = 1 - \exp(-qE)$$

Catchability was set at 0.09 ha·angler-day^{-1} (Cox 2000).

Since HR is, in effect, a density-independent mortality factor, analytical solutions can be derived for angling quality and yield as functions of effort at the fished equilibrium. Equilibrium spawner numbers at the fished equilibrium (N_e) can be obtained by replacing α and β in eq. 1 with $\alpha' = \alpha(1 - \mathrm{HR})$ and $\beta' = \beta(1 - \mathrm{HR})$ and setting $N_t = N$.

$$(3) \qquad N_e = \beta' - \beta'/\alpha'$$

For particular values of α, β, and HR, substituting eq. 3 into eq. 1 gives recruits at the fished equilibrium (N_{te}). Yield in the fishery (Y) is the difference between recruits and spawners at the fished equilibrium

$$(4) \qquad Y = N_{te} - N_e$$

and angling quality (NPUE, fish·angler-day^{-1}) is the ratio of Y to effort

$$(5) \qquad \mathrm{NPUE} = Y/E$$

Since Y is a function of E, α, β, and q, then equilibrium NPUE can plotted as a function of E, the demographic parameters α and β, and the constant q. The IFD equilibrium for a given set of demographic parameters occurs where E is such that NPUE equals the regional average (2.07 fish·angler-day^{-1}; Sisme 1988). Given E, then N_e and Y can be calculated for each combination of α and β using eqs. 1–4.

Spawner densities, yields, and harvest rates under maximum sustained yield (MSY) conditions can be derived analytically as functions of α and β (Ricker 1975). Effort at MSY is derived by substituting the MSY harvest rate into eq. 3 and MSY angling quality can then be calculated using eq. 5.

Size-structured demography

The age-structured simulation model runs on an annual time step that mimics the annual sequence of events for rainbow trout in lakes. Rainbow trout spawn in streams where they rear as juveniles for 0–2 years before migrating to the lake and growing to adult size (Northcote 1969). Spawning takes place in May and most of the harvest is taken in May, June, and July. In the simulation model, all newly emerged fry enter the lake in July at a size of 2.6 cm at the start of the annual cycle. Effective density is calculated at this point from the numbers and lengths of fish in each age-class. Growth and survival for the coming year are calculated for each age-class. In May, all fish greater than age 2 mature, and spawning mortality is applied. Egg production is calculated using the lengths after growth and the numbers of mature fish are calculated after size-dependent mortality but prior to spawning mortality and harvest. Harvest is applied to the population in each age-class that remains after the application of spawning and size-dependent mortality. After harvest, the remaining fish graduate into the next age-class and the annual cycle is repeated. Maximum age is 7, which is implemented as 100% spawning mortality at the end of the seventh year of life. The number of newly emerged fry is the product of egg production and egg–fry survival. Egg–fry survival is assumed to be density independent and covers the period from just prior to egg deposition to just after the age-0 fish enter the lake. Stock productivity is varied by assigning a density-independent egg–fry survival that covers an eightfold range (1%, 2%, 4%, and 8%). Using the model, we evaluate the status of populations at equilibrium over a range of stock productivities (analogous to α), habitat capacities (analogous to β), and effort densities. We compare the status in terms of fish densities, growth rates, yields to the fishery, and angling quality for three equilibriums. At the unfished equilibrium, a minimal effort (0.001 angler-days·ha^{-1}) is used to establish angling quality. The MSY state is evaluated by searching for the effort that maximizes biomass yield. The IFD state is evaluated by searching for the effort that results in an angling quality equal to that experienced by anglers on Region 3 lakes.

Density-dependant growth is modeled as a function of effective density (ΣL^2) of the fish in the lake rather than more conventional measures such as numerical density (ΣL^0) or biomass density (ΣL^3). Walters and Post (1993) showed that the effective density can be used to represent the total demand for food resources by individuals that vary in size. Using empirical data from lakes that varied in both density and size structure, Post et al. (1999) demonstrated that effective density explains a higher proportion of among-lake variance in growth than either numerical density, which weights small fish heavily, or biomass density, which weights large fish heavily.

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Effective density is used to model density-dependant growth using Walford plots that represent annual growth with the equation

$$(6) \qquad L_{i+1} = a + bL_i$$

where L_i is the length at age i, a is the Walford intercept, and b is the Walford slope. Assuming that competition among size-classes is symmetrical (i.e., based simply on their capacity to consume food resources), Walters and Post (1993) demonstrated that a varies as a linear function of effective density but b does not. The result is that growth can be described by a series of parallel lines that correspond to variations in density (Fig. 1). As density approaches zero, both growth rate and a approach a maximum. At very high densities, a approaches zero, growth rates are negative, mortality increases, and density falls. An estimate of b (mean 0.71, SE 036) was obtained from Walford plots of multimesh gillnet samples of rainbow trout from 34 lakes in southern British Columbia (B.C. Ministry of Sustainable Resource Management, unpublished data, available at http://srmapps.gov.bc.ca/apps/fidq/). Only a few (three to six) age-classes were present in each lake and estimates of b from individual lakes were homogeneous (analysis of covariance (ANCOVA), p = 0.087).

If the Walford b is constant, density-dependent growth can be modeled by expressing the Walford a as a function of effective density. The relationship between effective density and the Walford a in eq. 6 was parameterized using a linear regression (r^2 = 0.82) fitted through data (Fig. 2) collected by Post et al. (1999).

$$(7) \qquad a = 18.8 - 2.8 \times 10^{-5} \times D$$

where D is the effective density (square centimetres per hectare) at the start of the year and 18.8 (cm) is the maximum value of a that is observed at very low densities. The maximum growth rate (a = 18.8 cm when D = 0) is presumably controlled by factors such as the genetic characteristics of the stock and the physical characteristics of the environment (e.g., temperature) rather than food density. The minimum observed growth rate (a = 5 cm when density = D_{max}) is presumably controlled by factors such as the minimum length at maturity and the minimum length needed to survive the first winter.

To simulate a range of habitat capacities (analogous to β in eq. 1), we varied the slope of this relationship (eq. 7). The rate at which the Walford intercept a declined with density (i.e., the slope in eq. 7) was set at four multiples (0.25, 0.5, 1, and 2 times) of the slope (-2.8×10^{-5}) estimated from the data in Fig. 2. The minimum value for a (i.e., the intercept in eq. 7) is assumed to be constant, which implies that D_{max} is set at 4, 2, 1, and 0.5 times that observed by Post et al. (1999). The biological interpretation is that, at low habitat capacity, growth will decline rapidly with density (i.e., D_{max} is small) and at the highest habitat capacity, growth declines slowly with density (i.e., D_{max} is large). When combined with the stock productivity range described above, this range of habitat capacity produces densities and size structures that are within the range observed in natural lake populations of rainbow trout in southern British Columbia.

Survival is a function of initial length of cohorts of rainbow trout and the density of fish in the lake (Fig. 3). Rainbow trout from five size groups were stocked in nine experimental lakes that varied in density among lakes and among years (see Post et al. (1999) for details). The initial size of cohorts was manipulated through a combination of incubation temperate and size selection. Mean lengths of the five groups were 2.6, 3.6, 8.8, 10.4, and 11.9 cm. The range of lengths within each group was <0.5 cm. In the model, as in the empirical data, the observed annual survival for fish of age-class i (S_i) declined exponentially with total density of all age-classes (D) and an exponent (m_i) that is related to size.

$$(8) \qquad S_i = S_{imax} \exp(-m_i D)$$

This relationship was parameterized using annual survival data for the five size-classes of age-0 and age-1 trout. Maximum annual survival rates were empirically estimated as a saturating function of length at the start of the year (Fig. 4*a*).

$$(9) \qquad S_{imax} = 0.49\left[\frac{L_i - 1.81}{1 + 0.49(L_i - 1.81)}\right], \quad r^2 = 0.95$$

where L_i is the length (centimetres) for fish of age i at the start of the year fitted to the intercepts of the empirical relationships between annual survival and initial total density (Fig. 3) for five size-classes of juvenile trout. The empirical relationship between the exponent m_i and L_i was

Fig. 1. Density-dependent growth of lacustrine rainbow trout in southern British Columbia as represented by Walford plots when competition among size-classes is symmetric (Walters and Post 1993). The slope (b) of all three lines is 0.71, which represents the average slope from gillnet samples from 34 local lakes and is assumed to not vary with effective density ($cm^2 \cdot ha^{-1}$). Maximum growth (thick solid line) represents an extrapolation of the intercept (a) to zero density using the data of Post et al. (1999). At high densities, the minimum growth (dotted line) is limited by the minimum size at maturity and the size needed to survive the first winter. Growth at an effective density of 200 000 $cm^2 \cdot ha^{-1}$ (dashed line) lies between these two extremes. The thin solid line represents the one-to-one relationship. The asymptotic sizes are 64, 17, and 45 cm. If all fish are 30 cm long, 200 000 $cm^2 \cdot ha^{-1}$ is equivalent to about 220 fish·ha^{-1} or 68 kg·ha^{-1}.

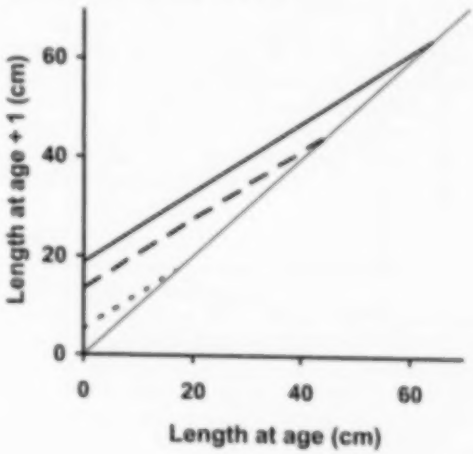

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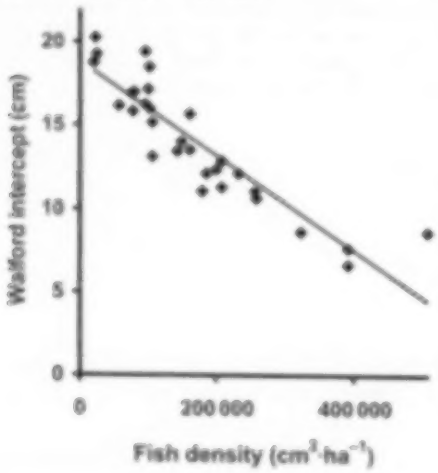
Fig. 2. Walford intercepts (a in eq. 2) as a function of effective density calculated from the data of Post et al. (1999). Each data point represents the growth of a group of age-0 fish. Lengths at the end of the growing season were estimated directly from field data. Length at age 1 was calculated by adding an increment that represented growth between the end of the growing season and the anniversary of lake entry in early July. This increment was estimated using a relationship between age-1 growth rate (mm·month^{-1}) and effective density. The Walford intercept for each group is calculated assuming a slope (b in eq. 6) of 0.71 and a length at lake entry of 2.6 cm.



(10) $m_i = -3.27 \times 10^{-6} \ln(L_i) + 1.21 \times 10^{-5}$, $r^2 = 0.94$

where the observed m_i (Fig. 4*b*) are again derived from survival versus density relationships for five size-classes (Fig. 3). To simulate the effect of different habitat capacities on survival, the m_i derived from the empirical data was multiplied by 0.25, 0.5, 1, or 2. The effect of this is that the density necessary to depress survival to a given value is 4, 2, 1, or 0.5 times the empirical estimate from eq. 10. The biological interpretation is that, at low habitat capacity, survival will decline rapidly with density (i.e., m_i is large) and at the highest habitat capacity, survival declines slowly with density (i.e., m_i is small).

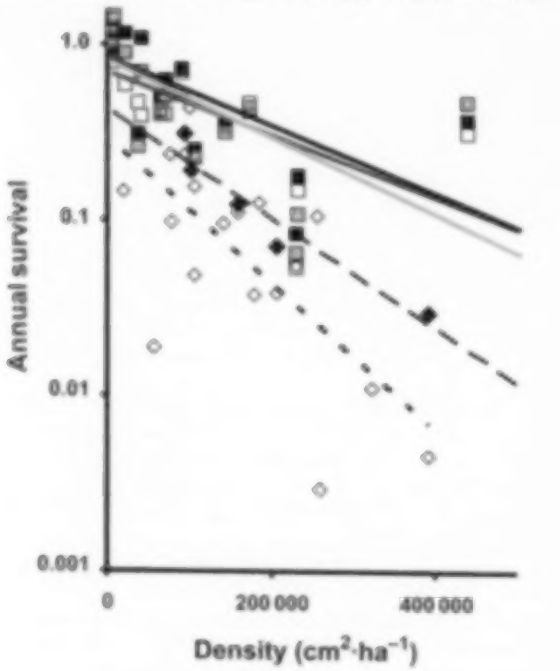
A postspawning survival of 30%, with a maximum age of 7, was chosen to match the age distribution in naturally spawning populations of lightly exploited rainbow trout in British Columbia. Age at first maturity was assumed to be constant at 3 years (Cox 2000). Egg production per mature adult of age i (F_i) was derived data collected by local hatcheries.

(11) $F_i = \exp[2.9 \ln(L_i) - 10.6]$, $r^2 = 0.92$

where L_i is the length (millimetres).

The harvest process is modeled in a manner similar to that of Cox and Walters (2002) who analyzed fishing effort, exploitation, and size-selectivity data from eight rainbow trout fisheries in lakes in southern British Columbia. Annual angler effort (E, angler-days per hectare) is a driving variable that is assumed to be constant in a given run. Cox and

Fig. 3. Annual survival of five size-classes of fish as a function of effective density derived from data collected by Post et al. (1999). Each data point represents the survival of a group of age-0 or age-1 fish. Initial lengths of each size-class are 11.9 cm (solid squares, solid line), 10.4 cm (shaded squares, dark shaded line), 8.8 cm (open squares, light shaded line), 3.6 cm (solid diamonds, dashed line), and 2.6 cm (open diamonds, dotted line). Lines fitted through each set of points are of the form $\ln(S_i) = \ln(S_{max}) - m_iD$ and have r^2 values that range from 0.31 to 0.92.



Walters (2002) derived a two-parameter fishing mortality rate (f) function of the form

(12) $f = qvE/(2v + qE)$

where q is a catchability coefficient and v is the instantaneous turnover rate between pools of available and unavailable fish. This model attempts to account for the fact that catch rates in sport fisheries are somewhat dependent on fish reactivity (i.e., to lures of various types) and the relative distributions of fish and anglers, both of which change (at rate v) over short time scales. Equation 12 is thus an instantaneous fishing mortality rate, which can be used to compute the annual exploitation rate for fully vulnerable fish (U_{max}).

(13) $U_{max} = 1 - \exp(f)$

Tagging data collected by Cox (2000) indicates that exploitation rate of an age-class (U_i) is a sigmoid function of its length.

(14) $$U_i = U_{max}\left(\frac{L_i^w}{L_i^w + L_{half}^w}\right)$$

where L_{half} is the length at which 50% of age-class i fish are vulnerable to harvest and w is the steepness of the curve at

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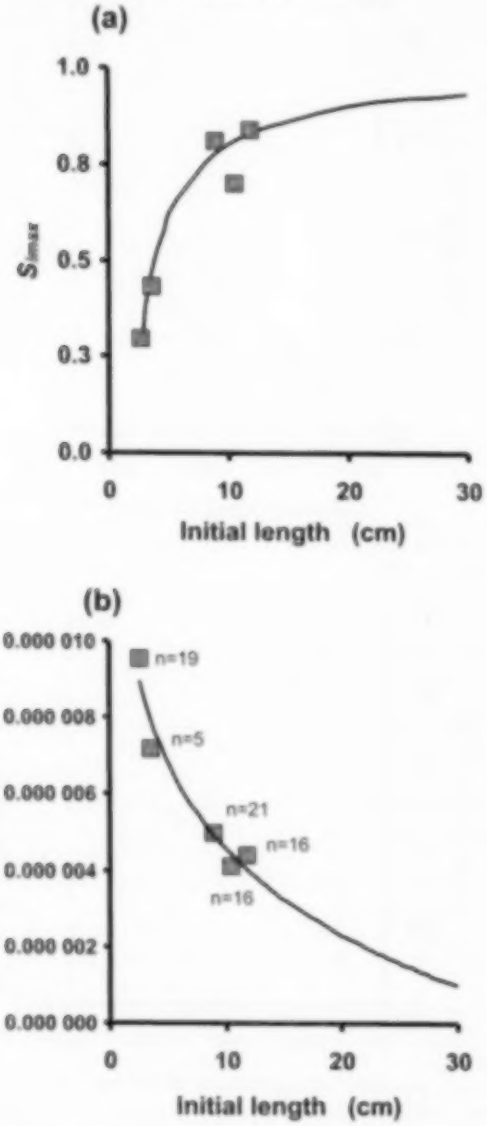
Fig. 4. Relationships between (*a*) maximum annual survival (S_{max}) and (*b*) the rate of change of mortality with density (m_s) and mean initial length as derived from the intercepts and slopes of relationships in Fig. 3. Each point represents a size group where annual survival was repeatedly measured across a range of densities to develop a relationship between initial length and annual survival across a range of densities. In Fig. 4*b*, the number of survival estimates for each point is given as *n*.



$L_{0.5E}$. Except for effort, harvest parameter values are those used by Cox (2000). They are $q = 0.09$ ha·angler-day^{-1}, $v = 1.61$·year^{-1}, $L_{0.5E} = 20$ cm, and $w = 8$. With these parameters, the maximum exploitation rate at very high effort levels (U_{max}) is 80% (rather than 100%) of the fully vulnerable fish per year. Over the range capacities and egg–fry survivals used in the model, maximum yields in the model are less than the maximum yields (~120 kg·ha^{-1}; B.C. Ministry of Sustainable Resource Management, unpublished data, available at http://srmapps.gov.bc.ca/apps/fidq/) observed for lakes in this region.

In the size-structured simulations, the anglers' perception of identical angling quality is defined using an isopleth on a plot of catch rate versus fish size. To empirically describe the trade-off that anglers make between average length and NPUE, we parameterized an isopleth for southern British Columbia interior rainbow trout lakes using mean length and NPUE data collected in a variety of creel surveys over the last 15 years on lakes in Region 3. We excluded three lakes where the number of interviewed anglers was low (<100 angler-hours) and two lakes that were not directly accessible by road. Data from winter ice fisheries were also excluded. The reduced data set from 38 lakes reflects the angling quality conditions experienced by the population of anglers that fish lakes in this general area during the ice-free season. If anglers can move freely among these lakes, IFD theory suggests that a curve fitted through these points can be assumed to represent an isopleth of equivalent angling quality for lakes that differ in fish density and size structure. For comparison, we have also included data from 15 lakes in British Columbia Management Region 5.

Results

A simple numerical model

The implications of an effort-driven IFD equilibrium can be seen in the relationships of angling quality and yield versus effort (calculated using eqs. 1–5) for three fish populations that vary in habitat capacity (β) but share a common stock productivity (α) and catchability (q) (Fig. 5). At a given level of effort, both angling quality and yield increase with β. In each case, angling quality declines linearly with effort and the IFD equilibrium occurs where this line of declining angling quality intersects the regional average angling quality (Fig. 5). It is important to note that there is no reason to expect that the IFD-driven equilibrium should correspond to the peak of the yield curve (i.e., MSY). The IFD equilibrium is driven by the angling quality experienced by individual anglers rather than the total number of fish captured by all anglers. For high values of β, IFD yields are less than MSY because high densities of fish attract high levels of effort, which result in higher than optimal harvest rates (Fig. 5). For low values of β, IFD yields are also less than MSY because angling quality is not high enough to attract the effort necessary to produce MSY. At very low values of β, effort is expected to be zero, since angling quality at zero effort is less than the regional average.

Similar results are predicted when both α and β vary. MSY increases with both α and β, but yield under the IFD assumption is relatively insensitive to increases in β (Fig. 6*a*). Since MSY is by definition a maximum, the IFD yields are almost always less than MSY (Fig. 6*b*). However, this simple model also illustrates that, in many cases, yields are only a fraction of those possible under optimal management control. At low values of α and β, angling quality (Fig. 6*b*) is not high enough to attract the amount of effort necessary to produce maximum yields. Alternatively, when α and β are high, then angling quality (NPUE) at MSY is much greater than the regional average, which attracts exces-

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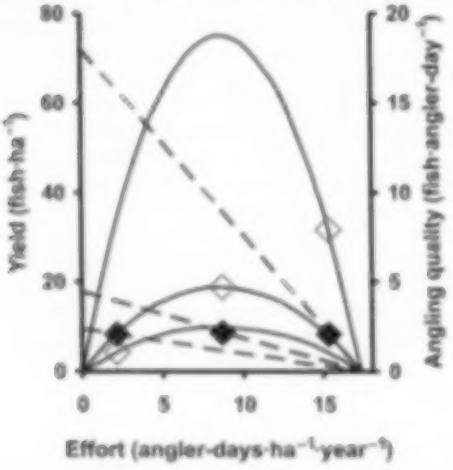
Fig. 5. Yield (solid lines) and angling quality (broken lines) predicted from the simple analytical model for three populations that share a common stock productivity (α = 4 recruits-spawner^{-1}) and catchability (q = 0.08 ha-angler-day^{-1}) but vary in habitat capacity (β = 300, 75, and 40 fish-ha^{-1}). For each curve, the IFD equilibrium yield (open diamonds) and angling quality (solid diamonds) have been calculated by assuming that the IFD equilibrium point is where angling quality equals the regional average in British Columbia rainbow trout lakes (2.07 fish-angler-day^{-1}).



sive effort that drives the spawner populations at the IFD equilibrium below MSY levels. These populations are capable of sustaining higher yields but do no do so because of systematic recruitment overfishing.

Angling quality and harvest rates in size-structured populations

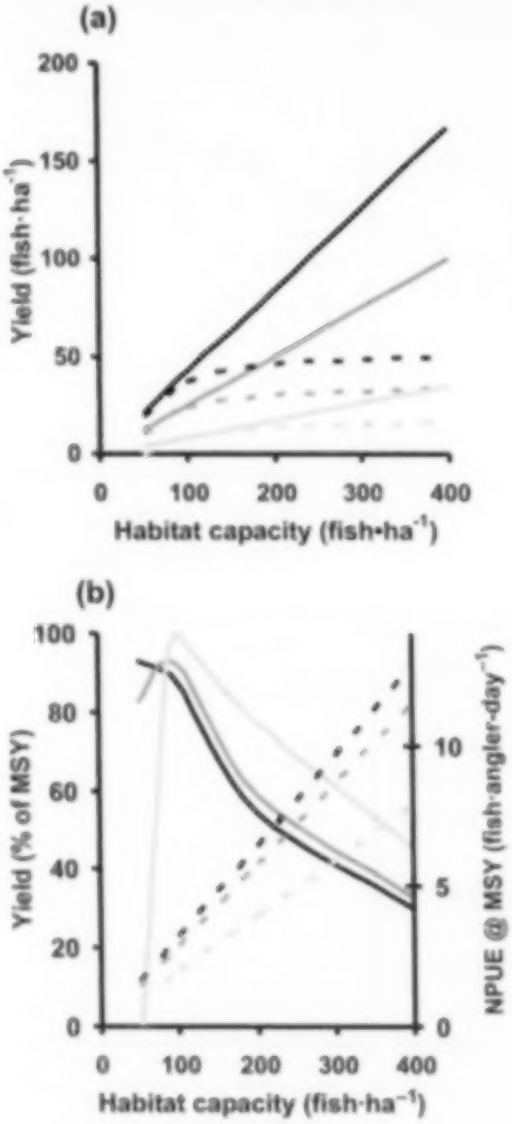
Empirical data on angling quality and effort are consistent with the prediction, based on IFD theory, that angling quality should be similar among lakes within a region but higher on lakes that are farther from population centers. The relationship between catch rate and fish size is significant but differs among regions (ANCOVA, $p < 0.001$) (Fig. 7). Lakes in Region 5, which are farther from British Columbia's major population center (Greater Vancouver), have a numbers–size trade-off that is similar in form to Region 3, but with higher angling quality. The higher angling quality in Region 5 is associated with a lower density of anglers (8 versus 45 angler-days-ha^{-1}-year^{-1}), higher mean depths (9.9 versus 8.5 m), and lower total dissolved solids (167 versus 191 ppm).

Angling quality in Region 3 can be described as a power function:

$$(15) \quad \text{NPUE} = 1\,320\,000 \times L_c^{-4.17}, \quad r^2 = 0.70$$

where L_c is the average length of fish in the creel. These parameters are used to define the IFD equilibrium in the size-structured model. This relationship suggests that anglers in Region 3 place a premium on size. When fish are small the observed NPUE is on average higher and when fish are large the observed NPUE is on average lower than that predicted if the numbers–size trade-off was simply proportional to weight (Fig. 7).

Fig. 6. (*a*) Yield achieved at MSY (solid lines) and at an IFD equilibrium with a target angling quality of 2.07 fish-angler-day^{-1} (broken lines) and (*b*) yield at the IFD equilibrium as a percentage of MSY (solid lines) and angling quality at MSY (broken lines) as function of habitat capacity (β). In each case, results for three values of stock productivity (α = 2, 4, and 8 recruits-spawner^{-1}) are given with darker lines representing higher values of α.



The size-structured population dynamics model produced stable equilibriums in the unfished (pristine) state over the full range of habitat capacity and stock productivity. Density increases with both productivity (egg–fry survival) and capacity (D_{max}) (Fig. 8*a*). Growth declines with stock productivity because higher density populations grow slower at a given lake capacity (Fig. 8*b*). Growth does not depend on capacity because the effect of higher densities, at higher habitat capacity, is exactly balanced by the increases in habi-

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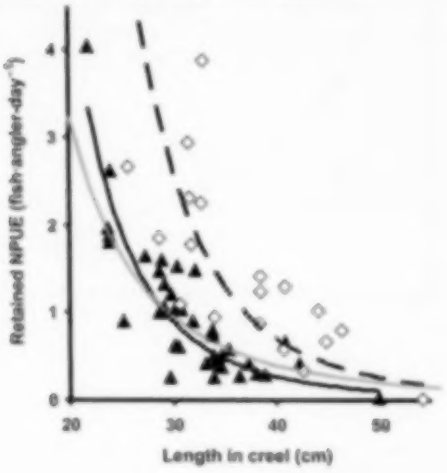
Fig. 7. Angling quality for 38 lakes in British Columbia Management Region 3 (triangles) and 15 lakes in British Columbia Management Region 5 (diamonds). The solid line is the best-fit power function (NPUE = 1 320 000 × $L_c^{-4.17}$, r^2 = 0.70) for the Region 3 data points. The broken line is a similar power function fitted to the Region 5 points (r^2 = 0.58). The shaded line is the best-fit line though the Region 3 data points that assumes a constant weight of fish per day on all lakes.



tat capacity. This outcome results from the direct proportionality between mortality and growth as a function of capacity in eq. 10.

When linked to the population model, the harvest model produces stable equilibriums (with constant effort) and an asymmetrical, dome-shaped yield curve over a range of angler effort (Fig. 9*a*). The MSY equilibrium (kilograms per hectare) can be estimated from this curve after using the relationship in eq. 15 to express yields in standard units to account for angler preferences for larger fish. Effort levels that result in an angling quality that lies somewhere on the equal quality isopleth (Fig. 7; eq. 15) can be used to define the position of IFD equilibrium (Fig. 9*b*). The IFD equilibrium conditions involve both a biological equilibrium (i.e., spawners = recruits) and an angler effort equilibrium because a lake is assumed to attract effort if angling quality lies above the angling quality isopleth and lose effort if angling quality is below the isopleth.

The trajectory followed by a hypothetical lake (D_{max} = 452 000 cm^2·ha^{-1}, egg–fry survival = 2%) under increasing amounts of effort, expressed in terms of the angling quality at equilibrium, can be used to illustrate the equilibrium process (Fig. 9*b*). In this case, pristine angling quality consists of an NPUE of just under 4 fish-angler-day^{-1} for fish that are 28.6 cm long. With increasing effort, density of fish in the lake declines and growth rates improve but the average size of fish is relatively stable because harvest rate is assumed to be a steep, sigmoid function of fish size (eq. 14). NPUE declines rapidly and sustained effort levels that are greater than 15 angler-days·ha^{-1} drive angling quality below the equal quality isopleth. Harvest pressure alone cannot drive the population to extinction because mortality has been assumed to be smoothly compensatory and anglers leave the lake if angling quality falls below the isopleth.

A comparison of equilibrium conditions for three system states (pristine, MSY, and IFD) over a range of stock productivity and habitat capacity suggests that large differences can be expected for many combinations. As in the simple numerical model, angling quality under MSY conditions is most strongly depressed (relative to pristine values) for higher productivity stocks but is independent of lake capacity (Fig. 10*a*). By definition, IFD angling quality is the same on all lakes but, when expressed as a fraction of pristine quality, IFD angling quality is depressed at both higher productivity and higher capacity. High capacity and stock productivity result in high densities of large fish under pristine conditions. As a result, pristine angling quality is very high and the difference between these and the IFD quality (eq. 15) is very large. IFD quality is often less than MSY quality and, in extreme cases, IFD angling quality is a small fraction of MSY angling quality.

For many combinations of stock productivity and habitat capacity, yields under the IFD equilibriums are substantially less than MSY (Fig. 10*b*). On low-capacity lakes, yields are low relative to MSY because angling quality at MSY is less than IFD angling quality. As a result, harvest pressure on these lakes at the IFD equilibrium is not high enough to maximize yield. Furthermore, if pristine angling quality is below the equal quality isopleth, angler effort should be close to zero. On lakes with high capacities, angling quality at MSY is well above the equal quality isopleth. Under IFD conditions, this higher quality attracts more angler effort, which depresses spawning populations to below the optimum and results in lower yields because the stock is overfished. IFD yields approximate the MSY only when angling quality at MSY lies close to the equal quality isopleth.

The biological characteristics of the population are also strongly impacted by the high harvest rates that are needed to drive the system to the IFD equilibrium. For the highest lake capacities, growth rates are close to the maximum over the full range of stock productivities (Fig. 10*c*). These high growth rates are the result of severe depressions in spawner densities to as little as 2% of pristine conditions (Fig. 10*d*). In general, overfishing at the IFD equilibrium results in much larger changes in biological characteristics and angling quality than those observed in yield.

Discussion

IFD theory predicts patterns in angling quality among lakes and regions that are similar to those that we observed. Within a region, most of the variance in catch rate is explained by differences in fish size and, as a result, angling quality can be described by an isopleth of NPUE versus fish size. The position of individual lakes along this numbers–size isopleth is determined by factors, such as the quality of juvenile habitat, that affect recruitment of trout but are unrelated to angler behavior. In contrast, factors that can be linked to angler behavior, such as travel time to the lake, are expected to affect angling quality. In our study area, angling quality was higher in Region 5, which was farther from the major population center; even though total dissolved solids and mean depth suggested that lake productivity of the lakes in this

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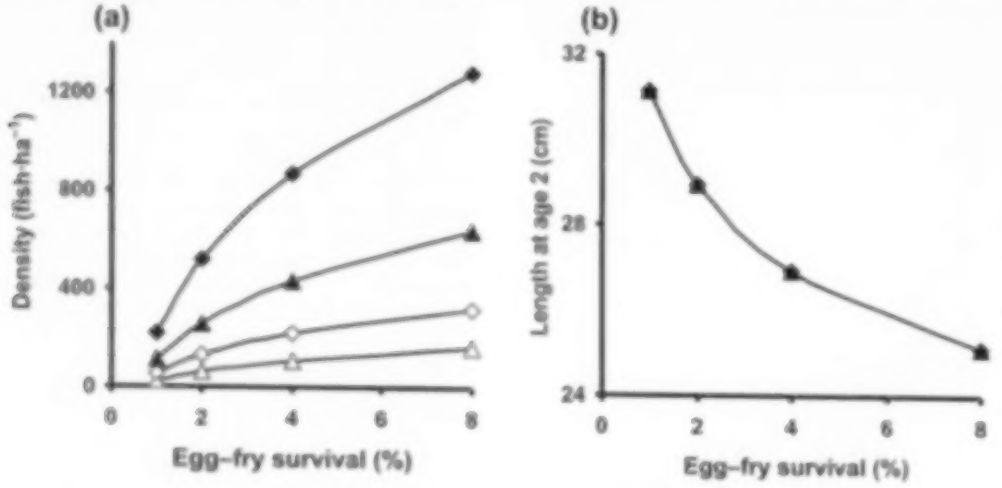
Fig. 8. Variation in (*a*) numerical density and (*b*) growth among modeled populations of rainbow trout modeled over a range of stock productivity (egg–fry survival) and habitat capacities. Lake capacities are 0.5 times (open triangles), 1 times (open diamonds), 2 times (solid triangles), and 4 times (solid diamonds) the standard capacity derived from the lakes used by Post et al. (1999). These values represent stable equilibriums under unfished (pristine) conditions.



region are about the same as in Region 3. Cox (2000) presented data on this fishery that are consistent with IFD theory; effort densities were linearly related to stocking density in both regions but the effort response per fish stocked was lower in Region 5. The distribution of harvesting effort in other fisheries is also consistent with the predictions of IFD theory (Gillis et al. 1993; Swain and Wade 2003). This dynamic view of angler behavior contrasts with the static portrayal of site selection where angling quality is simply one of many fixed factors that affect fishing site selection by anglers (Hunt and Ditton 1997).

The results of the simple numerical model clearly demonstrate the implications of IFD angler behavior for spatially structured fisheries where stock–recruitment parameters vary among stocks. Variable stock–recruitment parameters imply that optimum densities, and therefore catch rates, should vary among stocks. IFD harvesting behavior implies that actual catch rates, and therefore densities, should be similar, even among stocks that vary dramatically in optimal densities. The net result is that stocks are either underfished, when optimal densities are low, or overfished, when optimal densities are high. This in turn implies that, even if overall effort is not excessive, optimum harvest rates on individual stocks are unlikely to be achieved when anglers are free to move their harvesting effort among stocks.

The simple model assumes that catchability is constant with catch rates that are directly proportional to fish density. Empirical data suggest that catchability depends on both fish size and density (Cox 2000; Post et al. 2002). Since catch rate is the key link between recruitment dynamics and harvest dynamics, the implications of relaxing the constant catchability assumption need to be tested. The size-structured model incorporates size- and density-dependent growth, survival, and catchability with outcomes that are similar to those of the simple numerical model. This consistency suggests that our conclusions are relatively robust with respect to model structure.

The process of population regulation in harvested species has typically been considered in isolation from the dynamics of the harvesting effort. Biological management models predict densities and surplus production over a range of harvest rates, but the role of catch rates in determining the level of harvesting effort is rarely incorporated into the dynamics of population regulation. Our model of size-structured trout populations illustrates the effects of angler effort dynamics in a system where the biological mechanisms of population regulation are well documented. An empirical model of the biology, combined with an assumption of simple IFD angler behavior, predicts that open access management will rarely result in optimal populations of rainbow trout in lakes and, in some cases, densities will be depressed to a small fraction of pristine values. Lakes that are naturally capable of supporting high densities of large fish are the most likely to experience severe overfishing but stocks will rarely be driven to extinction if mortality is assumed to be smoothly compensatory. Post et al. (2002) suggested that this may often not be true and discussed a variety of depensatory mechanisms that may make it very difficult for fish stocks to recover after being depressed to very low levels. The focus on high-density, high-productivity populations contrasts with other threats that are generally seen to be more severe for small populations with low productivity (Lande 1993; Caughley and Gunn 1996).

Another clear prediction is that angler effort densities will be variable among lakes that vary in either habitat capacity or stock productivity but that angling quality will be much more uniform (Cox 2000; Post et al. 2002). Moreover, the observed variation in angling quality should be predictable from ancillary variables, such as remoteness, accessibility, or facilities that reflect attractiveness to anglers, rather than

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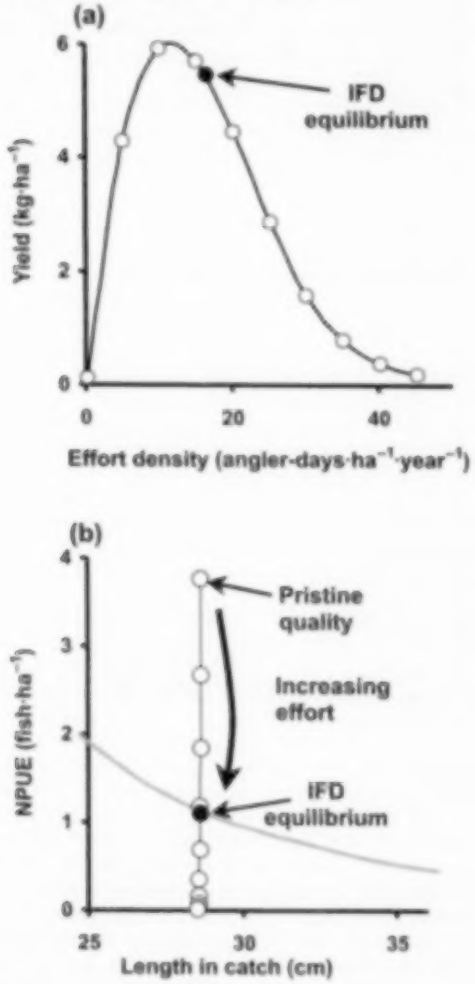
Fig. 9. (*a*) Yield as a function of effort for a model rainbow trout population. MSY is the peak of this curve. The arrow indicates the approximate position of the IFD equilibrium derived in Fig. 9*b*. (*b*) Angling quality (open circles) in a single lake under increasing amounts of effort. The equal quality isopleth (shaded line) is from the relationship described by eq. 15. The point where the two cross is a stable equilibrium driven by angler behavior under an IFD assumption. In both panels, the position of the open circles indicates effort increments of 10 angler-days·ha^{-1}·year^{-1}. In both cases, egg–fry survival is 2%, and capacity is the standard derived from the data of Post et al. (1999).



from characteristics of the lakes that affect the biology of the population. An exception will be lakes with little or no effort where angling quality will be lower than for other lakes. In these cases, angling quality will vary with pristine fish density and size structure, which are in turn a function of stock productivity and habitat capacity.

Both of these results can be generalized to a wide variety of fisheries. The theory behind the dynamics of harvesting effort has been empirically tested in some fisheries (Holland and Sutinen 1999) and it is clear that the effort dynamics play a critical role in determining current densities in many species. The fact that commercial fisheries with inadequate regulation have depleted many species to a fraction of their former abundance is generally recognized (Pauly et al. 2002) and the role of recreational harvest is now being documented (Post et al. 2002).

Although the process is general, the quantitative outcomes should not be. The position of the equal quality isopleth should vary with the costs of accessing the fishery. In more remote areas, such as Region 5 versus Region 3, we expect that the quality isopleth will be displaced away from the origin. Depletion will be less severe and there will be a greater likelihood that harvest rates will be close to zero because pristine angling quality lies below the isopleth. However, in locations near major population centers, we would predict severe depletion or even extinction of fish stocks when depensatory mechanisms are present (Post et al. 2002). In general terms, we expect that the position of the quality isopleth will be a function of a variety of factors such as remoteness, regulations, facilities, and aesthetics as well as preferences for individual fish species.

The biology of the system will also affect the outcome. In some species, biomass accumulates in older age-classes under pristine conditions and optimal populations consist of relatively high densities of large, old fish. If these high-density populations result in unusually high angling quality, harvesting effort will increase and deplete the stock. In Kananaskis Lake, for example, bull trout (*Salvelinus confluentus*) spawning populations expanded rapidly following the implementation of catch and release regulations that dramatically reduced both the effort and the mortality of captured fish (Mushens et al. 2001). Kananaskis Lake is less than a 2-h drive from the large city of Calgary, Alberta, and bull trout are long-lived salmonids that grow to almost a metre in length. In general, depletion should be expected to be more severe in long-lived, slow-growing species, such as lake trout (*Salvelinus namaycush*) or walleye (*Stizostedion vitreum*), than in short-lived species, such as the rainbow trout in this study.

We recognize the problems associated with focusing on the equilibrium when assessing the outcome of a dynamic process such as angler movements and fish population dynamics. Neither of these processes is expected to be particularly stable. Angler effort and distribution will be perturbed by factors such as the state of the economy, shifting social values, and changes in access to fishing opportunities. Fish populations will be affected by annual fluctuations in weather as well as longer term changes in climate and habitat. As a result, there is no particular reason to expect a system such as the one we have modeled to exist in a state of equilibrium. However, at least some of the processes involved strongly favor equilibrium. Anglers clearly use cues such as new access points, regulation changes, and the experiences of others to quickly focus in on exceptional angling quality that results from perturbations (Johnson and Carpenter 1994). Knowledge of angling quality is not perfect and varies among individuals. Differences in NPUE can be difficult to detect but differences in fish size should be more obvious (Parkinson et al. 1988). However, studious anglers with many connections in the angling community may be adept at de-

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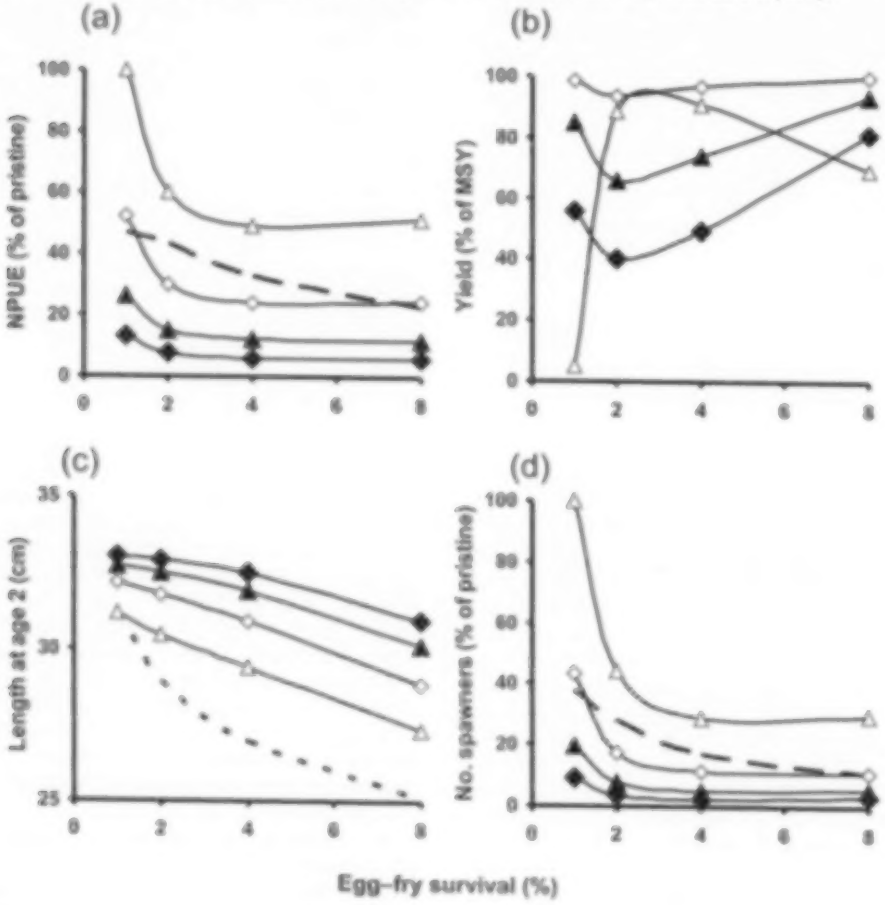
Fig. 10. (*a*) Angling quality (fish·h^{-1}) as a fraction of pristine conditions for the MSY (broken line) and the angler-driven IFD states. (*b*) Yield (kg·ha^{-1}) under the IFD state as a fraction of MSY. (*c*) Growth in the pristine (dotted line) and IFD states. (*d*) Spawner density relative to pristine under the IFD and MSY (broken line) modeled over a range of stock productivity (egg–fry survival) and habitat capacities. In all cases, solid lines represent IFD equilibriums. Lake capacities are 0.5 times (open triangles), 1 times (open diamonds), 2 times (solid triangles), and 4 times (solid diamonds) the standard capacity derived from the lakes used by Post et al. (1999). Angling quality is expressed in terms of catch rates of standard-sized fish (~30 cm). Both IFD and MSY yields are expressed in terms of kg 30-cm fish·ha^{-1}. MSY yields, pristine growth rates, and MSY spawner densities do not vary with lake capacity.



tecting transient opportunities with better angling. If these are regular seasonal occurrences, or are predictable from factors such as weather, we expect rapid response to exceptional opportunities.

The implications of IFD angler movement have parallels with the more familiar mixed-stock fishery problem (Paulik et al. 1967). In the conventional mixed-stock fisheries, several stocks are exploited in a single fishery with a single exploitation rate. If they differ in stock productivity, optimal harvest rates will differ among stocks and the combined yield from all stocks is below MSY. In mixed-stock fisheries involving IFD angler distribution, a mobile angler population holds all stocks at similar population densities. If stock productivities or maximum densities vary among stocks, then optimum population densities will differ among stocks and MSY cannot be achieved without restricting angler movement.

A key reason for the disconnection between sport fish management and angler dynamics may be the perception that management can effectively regulate fisheries without directly controlling angling effort. Biological models are often designed to provide reference points for the regulatory process rather than to explore the consequences of ineffective regulation. A variety of models (e.g., Luecke et al. 1994) have considered the effectiveness of alternative regulatory regimes but have not incorporated the dynamics of angler effort. Catch and release regulation is an effective conservation measure but pressure to permit harvesting and nonharvest mortality can both be serious problems when catch rates are high (Nelson 1998; Post et al. 2003). In some cases, the simple observation that anglers are less inclined to fish when catch rates are low has led to the idea that sport fisheries are "self-regulating", that is, anglers will leave a fishery that has been overharvested and thus allow it to re-

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cover (Hansen et al. 2000). Our results suggest that sport fishery management should be refocused onto strategies that deal with the negative consequences of unrestricted growth and movement of effort.

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Fatty acid biomarkers: validation of food web and trophic markers using ^{13}C-labelled fatty acids in juvenile sandeel (*Ammodytes tobianus*)

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Abstract: A key issue in marine science is parameterizing trophic interactions in marine food webs, thereby developing an understanding of the importance of top-down and bottom-up controls on populations of key trophic players. This study validates the utility of fatty acid food web and trophic markers using ^{13}C-labelled fatty acids to verify the conservative incorporation of fatty acid tracers by juvenile sandeel (*Ammodytes tobianus*) and assess their uptake, clearance, and metabolic turnover rates. Juvenile sandeel were fed for 16 days in the laboratory on a formulated diet enriched in ^{13}C16:0 followed by 14 days on a formulated diet enriched in ^{13}C18:3(n – 3). An exponential model was employed to estimate the uptake and clearance rates of recovered labelled fatty acids as a function of growth and fatty acid metabolism. The model predicted a faster uptake of ^{13}C18:3(n – 3) than ^{13}C16:0 (0.0353 and 0.0086·day^{-1}, respectively), consistent with a structural role of (n – 3) polyunsaturated fatty acids in cell membranes, whereas saturated fatty acids presumably play a larger metabolic role. Clearance and metabolic rates of assimilated ^{13}C16:0 were estimated as 0.0572 and 0.0211·day^{-1}, respectively. Lack of temporal trends in nonlabelled fatty acids confirmed the conservative incorporation of labelled fatty acids by the fish.

Résumé : Un problème crucial en science de la mer est la détermination des paramètres des interactions trophiques dans les réseaux alimentaires marins afin d'obtenir une compréhension de l'importance des contrôles descendants et ascendants sur les populations des groupes trophiques principaux. Notre étude confirme l'utilité des acides gras comme marqueurs du réseau alimentaire et comme marqueurs trophiques: nous avons utilisé des acides gras marqués au ^{13}C pour vérifier l'incorporation conservatrice des acides gras utilisés comme traceurs chez des jeunes lançons (*Ammodytes tobianus*) et évaluer leurs taux d'accumulation, de clearance et de remplacement métabolique. Nous avons nourri des jeunes lançons en laboratoire pendant 16 jours avec un régime élaboré enrichi en ^{13}C16:0, suivi d'un régime élaboré enrichi en ^{13}C18:3(n – 3) pendant 14 jours. Un modèle exponentiel nous a permis d'estimer les taux d'accumulation et de clearance des acides gras marqués récupérés en fonction de la croissance et du métabolisme des acides gras. Le modèle prédit une accumulation plus rapide de ^{13}C18:3(n – 3) que de ^{13}C16:0 (respectivement, 0,0353 et 0,0086·jour^{-1}), ce qui est en accord avec le rôle des acides gras polyinsaturés (n – 3) dans les membranes cellulaires, alors que les acides gras saturés jouent sans doute un rôle métabolique plus étendu. Nous estimons la clearance du ^{13}C16:0 assimilé à 0,0572·jour^{-1} et son taux métabolique à 0,0211·jour^{-1}. L'absence de tendances temporelles des acides gras non marqués confirme l'incorporation conservatrice des acides gras marqués par les poissons.

[Traduit par la Rédaction]

Introduction

One of the major challenges facing marine scientists at present is identifying and parameterizing the major processes governing the structure, functional diversity, and stability of pelagic ecosystems. The principal drive behind this challenge is the necessity for developing predictive capacities to develop management strategies for mitigating the impacts of global change on marine ecosystems, their roles such as exploited resources, and their feedbacks to the earth system via the sequestration of greenhouse gases. Parameterization of top-down and bottom-up controls on aquatic food webs represents one of the key issues in developing these predictive models of marine food webs as well as being critical for understanding how competition for resources and predation control the dynamics of key trophic players and thereby the functional biodiversity of marine ecosystems.

As a tool to parameterize these issues, fatty acid biomarkers enable us to identify the mode of feeding and the prey consumed by key trophic players at higher trophic levels (reviewed by Dalsgaard et al. 2003), hence identifying key interactions in marine food webs. The basis of the fatty acid biomarker approach is that aquatic predators deposit fatty acids obtained from their prey in a largely unmodified manner, thereby providing an integrated record of major prey items in their diet. As a result, fatty acid biomarker analyses have become an important tool for resolving trophic interactions in both marine (reviewed by Dalsgaard

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et al. 2003) and fresh water ecosystems (reviewed by Napolitano 1999). However, despite their widespread use, the conservative incorporation and turnover of specific fatty acid biomarkers have seldom been documented (see St. John and Lund (1996) and Kirsch et al. (1998) for examples). Such information is essential for applying specific fatty acid tracers and resolving the temporal dynamics of fatty acid biomarker signatures in predatory organisms.

To parameterize the dynamics of fatty acid biomarkers, the present study uses stable carbon isotope labelled fatty acids to (*i*) verify the conservative incorporation of specific fatty acid tracers by juvenile sandeel (*Ammodytes tobianus*), thereby documenting the applicability of fatty acid tracers for resolving food web processes, and (*ii*) assess the uptake and clearance rates of specific fatty acid tracers relative to variations in juvenile sandeel growth and fatty acid metabolism. Stable carbon isotope labelled fatty acids are nonhazardous and were therefore preferred over radioactive labelled fatty acids. Hence, stable carbon isotope labelled fatty acids are prepared by exchanging one or several of the ^{12}C isotopes along the acyl chain with heavier, stable ^{13}C isotopes. Labelled palmitic acid and α-linolenic acid, which are both commercially readily available, were used as specific tracers in the present study. Palmitic acid was chosen, as it is the major end product of the common lipid pathway, i.e., Type I fatty acid synthetase, and a precursor of all other commonly applied fatty acid biomarkers (Dalsgaard et al. 2003). It can be synthesized de novo by most organisms or may be obtained and incorporated from the diet. We therefore wanted to test if this fatty acid was incorporated directly, as modifications through further chain elongation and desaturation could invalidate the use of fatty acid biomarkers in the resolution of trophic interactions by disturbing the interpretation of other fatty acid tracer signals.

α-Linolenic acid was chosen as a representative of (n – 3) polyunsaturated fatty acids (PUFA), which are synthesized de novo mainly by marine primary producers (Cook 1996; Klein Breteler et al. 1999). It is a precursor of eicosapentaenoic acid and docosahexaenoic acid, which are essential for the normal growth and development of heterotrophic organisms, and it is used as a tracer of flagellated or green microalgae in combination with other PUFA (Dalsgaard et al. 2003 and references therein). Marine fish species studied so far are not able to convert α-linolenic acid to eicosapentaenoic acid and docosahexaenoic acid at any significant rate (e.g., plaice (Owen et al. 1972), turbot (Owen et al. 1975; Scott and Middleton 1979; Linares and Henderson 1991), red sea bream, rockfish, and globefish (Kanazawa et al. 1979), juvenile gilthead sea bream (Mourente and Tocher 1993*a*), and juvenile golden grey mullet (Mourente and Tocher 1993*b*)). They are hypothesized to have lost this capability because of a ready dietary source of eicosapentaenoic acid and docosahexaenoic acid, which are very abundant in marine microalgae (Sargent 1995; Sargent et al. 1995). Consistent with this, we hypothesized that juvenile sandeel would not further chain elongate and desaturate labelled α-linolenic acid.

Furthermore, we hypothesized that the labelled fatty acids would equilibrate in the fish at different rates depending on their metabolic and physiological role. Consistent with this, recent experimental evidence with rainbow trout (*Oncorhynchus mykiss*) has demonstrated that the dominant physiological roles of saturated and monounsaturated fatty acids are different (Weber et al. 2003). Hence, these experiments showed that oleate is incorporated more rapidly than palmitate into neutral lipids, suggesting that oleate plays a more prominent role in energy metabolism. Both fatty acids were, on the other hand, incorporated into phospholipids to the same extent, suggesting that they contribute equally to membrane turnover. In comparison, (n – 3) PUFA, including linolenic acid, are presumably incorporated preferentially into polar membrane lipids, where they function to assist the cells in reacting to external stimuli such as changing environmental temperatures and light regimes (Sargent et al. 1993; Cook 1996). The fatty acid composition of the juvenile sandeel was therefore hypothesized to change as a function of "structural" growth (especially PUFA) and metabolic turnover (especially shorter chain, saturated fatty acids).

Sandeel were chosen as the target species, as they, in particular, occupy a central trophic position in many shelf sea food webs, transferring biomass from plankton to higher trophic levels. For example, in the North Sea, sandeel (dominated by *Ammodytes marinus*) presently represent one of the key planktivorous fish species as well as a key prey species for piscivores such as cod and whiting (e.g., Read 1970; Wright et al. 1998 and references therein). Furthermore, the population dynamics of sandeel is probably influenced by hydrographic frontal systems (Møller et al. 1998; Wright et al. 1998), making them a candidate for linking fluctuations in climatic forcing to ecosystem dynamics. Frontal systems are horizontal boundaries between water columns with different properties, the dynamics of which are impacted upon by changes in thermal stratification and wind stress (e.g., Le Fèvre 1986; Simpson 1998). These systems are typically accompanied by enhanced primary production with a characteristic horizontal distribution of major groups of marine microalgae (Pingree et al. 1975; Cushing 1989; Richardson et al. 2000). The various microalgal groups are characterized by different fatty acid signatures (Dalsgaard et al. 2003), and the recognition of these signatures in sandeel may indicate where, in relation to a frontal activity, the fish have been foraging (St. John and Lund 1996; Møller et al. 1998). Coupled with information about fish growth and condition, this may potentially be used to test hypotheses on the effects of climatically driven variations in frontal hydrography and resultant plankton production on sandeel population dynamics.

The present study on juvenile sandeel represents to our knowledge the first attempt using stable carbon isotope labelled fatty acids to validate the conservative incorporation of fatty acid tracers and establish the uptake and clearance rates of specific fatty acid biomarkers in marine organisms.

Material and methods

Experimental setup

Approximately 1260 juvenile sandeel with a mean total length of 73 ± 6.5 mm were caught in Ålbæk Bay, Denmark, 21 June 2001, using a 40 m × 3.7 m black beach seine with a mesh size of 14 mm, narrowing down to 10 mm in the central third of the seine. The fish were transported in large, cylindrical containers with aerated seawater to the research facilities at the Danish Institute for Fisheries Research,

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Table 1. Composition of experimental diets.

Diet	Ecostart[a] (g)	Fish oil[b] (g)	Labelled fatty acids	Expected $\delta^{13}C$ (‰)	Expected APE[c]
Control	1000	50	—	–28	—
Enriched in tripalmitin-1,1,1-$^{13}C3$	1000	50	0.25 g	100	0.1
Enriched in linolenic acid-UL-$^{13}C18$	500	25	0.01 mL	500	0.6

[a]Low-lipid (6.9% w/w), 0.6 mm extruded, non-coated trout feed provided by BioMar A/S.
[b]Commercial fish oil provided by BioMar A/S.
[c]Atom percent excess = 100 x (A_{enr} - A_{bas}), where A = R/(R+1), *R* is the ratio of the heavier isotope to the lighter isotope, "enr" is the enriched sample, and "bas" is the baseline or unenriched sample (Scrimgeour 1997).

North Sea Centre, where they were transferred to two 1 m × 1 m × 0.3 m flow-through tanks at a density of approximately 2.1 fish·L^{-1}. There was no sediment in the tanks to prevent the fish from hiding and making it more difficult to wean them onto the experimental diet (see below). During acclimatization, the fish were maintained in seawater (30 ‰) of ambient ocean temperature (13.8–16.6 °C), a flow rate of 4 L·min^{-1}, and a simulated natural light cycle of 1 h : 16 h : 1 h : 6 h (dawn–day–dusk–night). During this period, they were weaned onto a modified commercial trout diet (Ecostart, BioMar A/S, see below), feeding initially with thawed *Artemia* sp. (Golden Gate Frozen Brine Shrimp, Novalek, Inc.) five times per day (120 g *Artemia*·tank^{-1}·day^{-1}), replacing gradually with the formulated diet. Four days prior to commencement of the feeding experiment, the fish were measured to the nearest 0.1 g and distributed randomly in fourteen 1 m × 1 m × 0.2 m flow-through tanks at a density of 0.45 fish·L^{-1}. The water flow rate was reduced to 3.2 L·min^{-1}, and the water temperature was fixed at 16 °C.

The actual feeding experiment ran for 30 days. During the first 16 days, all fish (less controls) were maintained on a diet enriched in labelled palmitic acid ($^{13}C16:0$; fatty acids are denoted using the shorthand notation *z*:*y*(*n* – *x*), where *z* is the number of carbon atoms, *y* is the number of double bonds, *n* represents the chain length, and *x* indicates the position of the first double counting from the terminal methyl group). On day 17, the fish were shifted to and maintained on a diet enriched in labelled α-linolenic acid ($^{13}C18:3(n-3)$) to assess the simultaneous incorporation of this labelled fatty acid and the clearance of $^{13}C16:0$. To determine how different growth rates would affect the uptake and clearance rates of labelled fatty acids, the fish were fed 1%, 2%, or 3% body wet weight·day^{-1}. The rations were estimated as constant proportions of the approximate biomass in the tanks and were adjusted throughout the experimental period as fish grew and were removed. Three replicate and one control tank were maintained for each of the three rations, and all treatment combinations were assigned randomly among 12 experimental tanks. Two fish were selected randomly from each tank 1 day prior to the start of the feeding experiment and their fatty acid stable carbon isotope ratios taken to represent the population at the start of the experiment. During the feeding experiment, nine fish were sampled from all tanks on days 8, 16, 24, and 30. In addition, nine fish were sampled from replicate 1 tanks on days 2, 10, and 18, replicate 2 tanks on days 4, 12, and 20, and replicate 3 tanks on days 6, 14, and 22.

Fish for analyses were placed in a container containing MS 222 (tricaine methanesulphonate). Upon termination of body motion, they were measured to the nearest 0.0001 g blotted wet weight and 0.1 cm total length and preserved at –80 °C in bags flushed with argon. Each sampling event took place after feeding to assure, from later examination of gut contents, that only feeding fish, i.e., those that consumed the formulated diet, were examined for fatty acid and stable carbon isotope content.

Two additional control tanks were maintained to derive a wet weight versus dry weight relationship. Fish from these tanks were sampled at intervals similar to replicate 2 tanks, measured as described above, dried for 48 h at 60 °C, and reweighed.

Preparation of diets

Diets were prepared as follows using fish oil provided by BioMar A/S. First, the oil was heated to 40–45 °C while stirring. Then, tripalmitin labelled with ^{13}C in the C1 position (counting from the carboxylic end of the acyl chain) (99%) (Medical Isotopes) or uniformly ^{13}C-labelled α-linolenic acid (98%) (Martek Biosciences Corporation) was added and stirring continued for another 30 min. The oils were subsequently coated onto low-lipid (6.9% *w/w*), 0.6-mm extruded commercial Ecostart trout pellets (BioMar A/S) using an atomizer. The pellets were blended to obtain a uniform distribution and an estimated final lipid content of 12.5% *w/w*. A control diet was prepared following the same procedure but excluding labelled fatty acids. We provide details on the quantities used in preparing the diets in Table 1. The prepared pellets were stored in 100-g aliquots at –80 °C until use.

Stable carbon isotope enrichment is reported in standard delta notation (δ) estimated as per mil (‰) deviation from a standard, i.e., $\delta^{13}C = [(R_{sample}/R_{PDB}) - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ and PDB is Vienna Peedee Belemnite. There exist no guidelines on the level of fatty acid stable carbon isotope enrichment that would lead to measurable effects in the fish. Hesslein et al. (1993) found that an overall dietary change in $\delta^{13}C$ of 4.9‰ was measurable in broad whitefish (*Coregonus nasus*) when fed on the new diet for 1 year. In the present study, dilution of the labelled fatty acids by other dietary ingredients had to be taken into account. In addition, the difference between the control and experimental diets had to be large enough to overcome foreseeable variations in growth and uptake rates by the individual fish and assure detectable trends within the relatively short feeding period. Moreover, the concentration of palmitic and α-linolenic acid in the commercial trout pellet and in the fish oil was not known beforehand. Hence, a content of 16% palmitic acid and 1% α-linolenic acid was assumed based on a literature survey of typical concentrations of these fatty acids in fish lipids, which constituted the major lipid ingredient in the diet. Adding the

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quantities of labelled fatty acids (summarized in Table 1), the final $\delta^{13}C$ values of the experimental diets were estimated at 100‰ and 500‰ (or ~0.1 and ~0.6 atom percent excess) for palmitic and α-linolenic acid, respectively.

Lipid and stable carbon isotope analysis

Extraction of samples for fatty acid analyses was performed on individual fish following the procedures outlined in Bligh and Dyer (1959). Prior to extraction, the head of each fish was removed and then passively extracted for 24 h in 2:1 (*v*/*v*) chloroform–methanol at –20 °C. The head was subsequently placed in 96% ethanol to allow the potential future analyses of otolith growth via daily increment widths. The stomachs were dissected from the frozen carcasses to avoid contamination of tissue fatty acid profiles from non-assimilated food and to assure that only fish that had consumed the formulated diets were analysed. The carcasses were subsequently homogenized in chloroform–methanol, adding the extracts from the heads and *n*-hexadecan-3-one (Sigma) as an internal standard.

The lipid class composition of the fish was examined to assure that only those that had been positively incorporating lipids were included in subsequent analyses. Hence, using cholesterol as a measure of structural growth (Håkanson 1989*a*) and triacylglycerol as a measure of nutritional condition (Fraser et al. 1987; Håkanson 1989*a*, 1989*b*), fish with a triacylglycerol/cholesterol ratio lower than the population mean at the start of the experiment were excluded, assuming that they had been starving. The lipid classes were separated by a thin-layer chromatography – flame ionization detector (Iatroscan MK-5). Samples were dissolved in *n*-hexane to a concentration of approximately 20 μg·μL^{-1} and spotted onto type S-III chromarods (1.4 μL) in duplicate using an autospotter (model SES 3200/IS-01). The rods were developed following procedures outlined in Parrish (1987). The flame ionization detector was operated at a hydrogen airflow of 2000 mL·min^{-1} and a scan rate of 30 mm·s^{-1}. Peaks were identified against known standards (Sigma) and integrated using Bruker-Franzen Analytik & SCPA ChromStar® version 3.24S software.

Fatty acid methyl esters were prepared by BF_3-catalyzed methylation, adding 21:0 methyl ester (Sigma-Aldrich) as an internal standard at this point in time. The fatty acid methyl esters were separated and the $^{13}C/^{12}C$ ratio determined by gas chromatograph – combustion – isotope ratio mass spectrometry (GC–C–IRMS) (Delta^{PLUS}, Thermo-Finnigan, Bremen, Germany). The samples were injected at 250 °C using a split ratio of 1:15 and separated on a fused silica capillary column (SP-2380, 60 m × 0.25 mm inside diameter, 0.20-μm film; Supelco Inc., Bellefonte, Pennsylvania). The temperature gradient was held at 70 °C for 3 min and raised to 150 °C at 15 °C·min^{-1}, to 169 °C at 1.5 °C·min^{-1}, to 173 °C at 0.5 °C·min^{-1}, to 188 °C at 3 °C·min^{-1}, and finally to 200 °C at 20 °C·min^{-1} and maintained for 14 min. The fatty acid methyl esters were identified against Nu-Check Prep (Elysian, Minnesota) GLC reference standards GLC-85 and GLC-401. Reproducibility of the results was ±1‰.

As only a limited number of samples could be processed on the GC–C–IRMS, only one of the three replicate series was selected and processed for labelled fatty acid analyses. To verify the choice of replicate series, samples from all tanks were obtained on day 24 of the experiment, processed, and the average labelled fatty acid compositions compared to reveal potential differences between replicate tanks.

Impact of growth and metabolism on the uptake and clearance of labelled fatty acids

Changes in the labelled fatty acid composition of the fish as a function of growth were modelled using a mixing equation developed initially for assessing the change in stable carbon isotopes in broad whitefish tissue (Hesslein et al. 1993)

$$(1) \qquad \delta_t = \delta_f + (\delta_0 - \delta_f)(W_0/W_t)$$

where δ_t is the $\delta^{13}C$ value of the fatty acid in the tissue at the time of sampling, δ_f is the $\delta^{13}C$ value of the fatty acid in the tissue in ultimate equilibrium with the new diet, δ_0 is the $\delta^{13}C$ value of the fatty acid in the tissue in equilibrium with the old diet, W_t is the weight of the fish at the time of sampling, and W_0 is the initial weight of the fish. Assuming that the growth patterns of juvenile sandeel approximate a sigmoidal form with the juvenile fish being in the "slow-growth, exponential part" of the curve, an exponential growth equation of the form

$$(2) \qquad W_t = W_0 e^{kt},$$

where k is the instantaneous growth rate, was fitted to logarithmically transformed, dry weight converted wet weights of fish fed different rations. Inserting the exponential growth equation into eq. 1 changes it to

$$(3) \qquad \delta_t = \delta_f + (\delta_0 - \delta_f)e^{-kt}$$

Using stable carbon isotope tracers, Tieszen et al. (1983) found that the metabolic turnover of carbon in different tissues of adult male gerbils (*Meriones unguienlatus*) shifted to a new diet was adequately described by an exponential model of the form

$$(4) \qquad Y = P_3 + P_1 e^{-P_2 T}$$

where Y is the $\delta^{13}C$ value of the tissue in question, P_1 is the total change in the $\delta^{13}C$ value of the tissue when it has changed from being in equilibrium with the old diet to being in equilibrium with the new diet, P_2 is the turnover rate of carbon in the specific tissue, P_3 is the asymptotic $\delta^{13}C$ value for that tissue on the new diet, and T is the time in days since the switch in diet. Hesslein et al. (1993) applied a similar function to describe the metabolic turnover of stable carbon isotopes in broad whitefish. Hence, assuming that the principles of this relationship apply to the metabolic turnover of labelled fatty acids and reexpressing eq. 4 in delta notation as

$$(5) \qquad \delta_t = \delta_f + (\delta_0 - \delta_f)e^{-mt}$$

where m is the fatty acid metabolic turnover rate, eqs. 3 and 5 may be added to model the ^{13}C-labelled fatty acid composition of sandeel, due to both growth and metabolism, as

$$(6) \qquad \delta_t = \delta_f + (\delta_0 - \delta_f)e^{-(k+m)t}$$

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Table 2. Results of Kruskal–Wallis tests (H) comparing average tracer levels in the three replicate series of fish fed different rations and sampled on day 24 of the experiment.

	^{13}C16:0			^{13}C18:3(n – 3)		
Ration (% body weight·day^{-1})	H	df	P	H	df	P
1	2.35	2	>0.05	0.58	2	>0.05
2	0.89	2	>0.05	5.77	2	>0.05
3	3.24	2	>0.05	1.08	2	>0.05

The fatty acid metabolic turnover rate is here the only unknown parameter and was estimated using a nonlinear iterative least squares algorithm in the SAS System for Windows®. Knowing k and m, the time interval for the labelled fatty acids to reach the midpoint between the initial and equilibrium level (doubling time or "half-life") in the fish tissue, i.e., $(\delta_f + \delta_0)/2$, was found as

$$t = \frac{\ln 2}{m + k} \quad (7)$$

Statistics

Statistical analyses were carried out in the SAS System for Windows® and in Microsoft® Excel 2000 applying a level of significance of 0.05 to all tests. Linear least squares regression analyses were used to convert wet weights to dry weights and to estimate growth rates of fish fed different rations after logarithmically transforming their dry weights. The estimated growth rates were subsequently compared in two-tailed t tests. To verify the choice of replicate series for fatty acid and stable carbon isotope analyses, the average tracer contents of fish from the three replicate series, obtained on day 24 of the experiment, were compared in Kruskal–Wallis tests. Finally, eq. 6 was fitted to the observed tracer levels in the fish using the MODEL procedure in SAS applying an iterative algorithm (GAUSS) to obtain the nonlinear least squares estimate of the unknown parameter (m).

Results

Mortality

No mortality was observed until day 14 of the experiment, approximately 1 month after captivity. After this point, dead individuals were observed in the tanks and a mortality rate of 0.001·day^{-1} was estimated, increasing to 0.214·day^{-1} by the end of the experiment. The fish that succumbed had not increased in wet weight relative to the population mean at the start of the experiment and in addition had no food in their gut, an occurrence suggesting that they were not consuming the formulated diet.

Wet weight versus dry weight

Based on the fish from the two additional control tanks, wet weights (WW) were converted to dry weights (DW) using the significant (least squares regression, $F_{(1,96)} = 3102$, $P < 0.0001$, $r^2 = 0.97$) linear relationship

$$\mathrm{DW} = -0.091 + 0.292\mathrm{WW} \quad (8)$$

Replicate series

Replicate 1 fish were selected at random for fatty acid and stable carbon isotope analysis. Confirming this choice, there were no significant differences (Kruskal–Wallis test, Table 2) in the average level of either ^{13}C16:0 or ^{13}C18:3(n – 3) in the three replicate series on day 24 of the experiment tested for fish fed different rations. The triacylglycerol/cholesterol ratio of replicate 1 fish is shown in Fig. 1. Those with a ratio lower than the population mean at the start of the experiment were excluded from further analyses, assuming that they had not adapted to the formulated diets and therefore had not incorporated the labelled fatty acids.

Growth rates

The estimated growth rates (k) of fish fed different rations (least squares regression) (Table 3) were not significantly different (two-tailed t test) (Table 4) from each other. The fish were therefore pooled under the assumption that there were no differences in growth between the tanks, and an overall growth rate of 0.0362·day^{-1} was obtained by applying a least squares regression analysis to the pooled data (Table 3; Fig. 2). Similar growth rates were probably an effect of hierarchy formation in the tanks, with dominant individuals attaining first access to the restricted diet (Jobling 1994), which occurred despite attempts to minimize this problem by hand feeding.

Model output

As for the growth data (Fig. 2), there was considerable scatter in the levels of labelled fatty acids exhibited in the fish (Fig. 3), which did not equilibrate with the diets within the experimental period. The δ_f values were therefore derived by combining information on diet enrichment and the fatty acid stable carbon isotope composition of the control fish. The δ^{13}C16:0 and δ^{13}C18:3(n – 3) values of the experimental diets were 135‰ (±8‰) and 540‰ (±18‰), respectively. In comparison, the δ^{13}C value of the two fatty acids in the control diet was –28‰ (±1‰). The control fish, which did not display any changes in δ^{13}C values over the course of the experiment, were depleted by 1‰ in ^{13}C16:0 and 8‰ in ^{13}C18:3(n – 3) relative to the control diet. Using these levels of trophic fractionation, expected δ_f values of 134‰ for ^{13}C16:0 and 532‰ for ^{13}C18:3(n – 3) were derived.

Applying eq. 6 and assuming a metabolic turnover of zero, i.e., using only growth to predict the uptake of labelled fatty acids, the predicted uptake of δ^{13}C16:0 was much faster than actually observed (Fig 3*a*). In comparison, the predicted uptake of δ^{13}C18:3(n – 3) (Fig. 3*c*) and clearance of δ^{13}C16:0 (Fig. 3*b*) were much closer to the observed data. Fitting the model to the data by finding the nonlinear least squares estimates of metabolism improved the fit considerably (Fig. 3). It was obvious, however, that many of the fish were growing suboptimally on the formulated diets, and the model was therefore also fitted to the top 25% of the population with respect to observed tracer levels (Fig. 4) to obtain more "realistic" rate estimates. The estimated rates of metabolism as well as the overall uptake and clearance rates derived by adding k and m are summarized in Table 5 together with the corresponding doubling times (for the uptake of labelled

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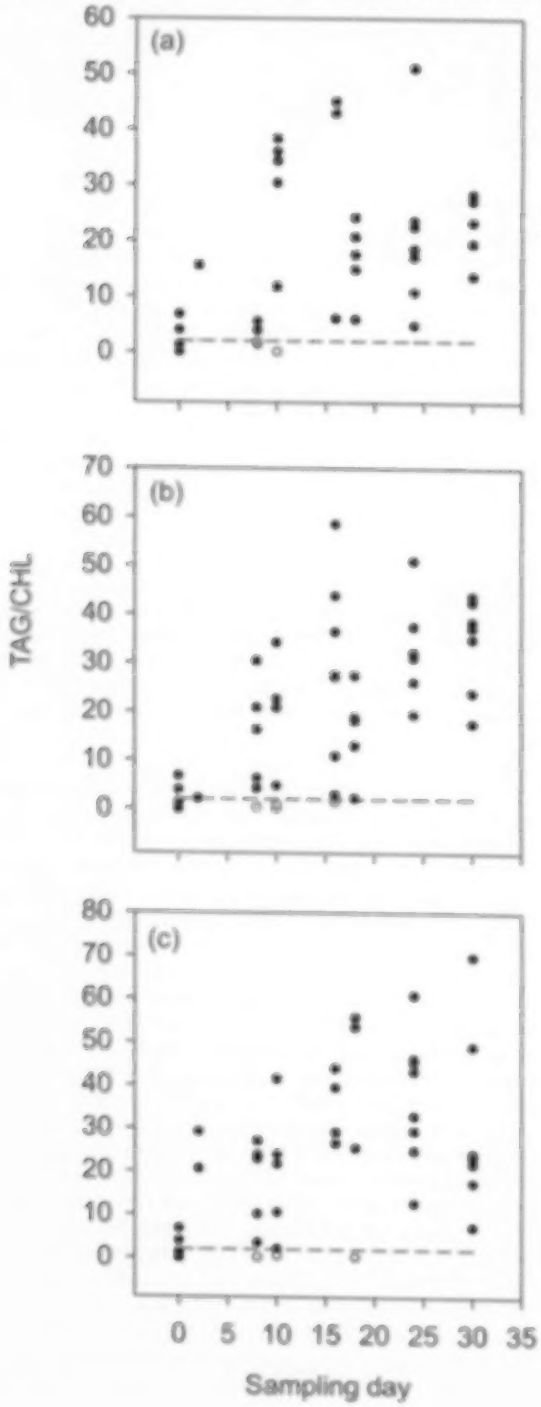
Fig. 1. Ratio of triacylglycerol (TAG) to cholesterol (CHL) versus sampling day in fish fed (*a*) 1%, (*b*) 2%, or (*c*) 3% of their body wet weight per day. Fish with a ratio lower than the population mean at the start of the experiment, indicated by the broken lines, were excluded from fatty acid and stable carbon isotope analyses. Solid circles, included; open circles, excluded.



palmitic and α-linolenic acid) or half-life (for the clearance of labelled palmitic acid).

Nonlabelled fatty acids

Visual inspection of the isotopic levels of other major fatty acids identified in the fish revealed no apparent temporal trends (Table 6), confirming that the labelled fatty acids were incorporated in a largely conservative manner.

Discussion

Despite considerable scatter in the data, presumably as a result of differential feeding, this study clearly demonstrates the potential of stable carbon isotope labelled fatty acids for verifying the incorporation of fatty acid tracers by fish, assessing their uptake and clearance rates, and estimating their metabolic turnover.

The model predicted that labelled palmitic acid would be incorporated much faster than actually observed when assuming a metabolic turnover of zero. In comparison, growth was a much better predictor of the uptake of α-linolenic acid, especially when modelling the top 25% of the population with respect to observed tracer levels. These differences suggest that a larger fraction of labelled palmitic acid than of α-linolenic acid was metabolized during uptake and (or) was not assimilated at all. Consistent with the latter, PUFA are generally more efficiently absorbed than monounsaturated and saturated fatty acids (Sigurgisladottir et al. 1992; Koven et al. 1994). Alternatively, the fish may have discriminated against the enriched fatty acids and more against palmitic acid than against α-linolenic acid. Palmitic acid was, however, only labelled in the C1 position, whereas α-linolenic acid was labelled in all C atoms. The faster uptake of labelled α-linolenic acid than of palmitic acid is therefore not consistent with a discrimination against enriched fatty acids.

The best fit of the model for predicting the uptake of labelled fatty acids was obtained with "negative metabolic" rate estimates. Such estimates make no sense in themselves but were the consequence of the excess level of incorporation predicted from growth alone. An estimate of metabolism cannot therefore be obtained from the uptake part of the experiment. It can, however, be obtained from the clearance component. Here, the clearance of assimilated, labelled palmitic acid observed when the fish were fed only labelled α-linolenic acid can be ascribed to the combined effects of metabolism and dilution through growth. The validity of the metabolic rate estimate presupposes that labelled α-linolenic acid was not reduced to, and hence mistaken for, labelled palmitic acid. Supporting this assumption, no temporal trends were observed in the $\delta^{13}C$ values of other major fatty acids identified in the fish. The experiment did not run long enough to obtain a metabolic turnover estimate and a clearance rate estimate of α-linolenic acid. However, growth (i.e., dilution) will surely be an important factor for the clearance of α-linolenic acid, given its structural role in cell membranes and the general faster uptake of PUFA than of saturated fatty acids (Sigurgisladottir et al. 1992; Koven et al. 1994). On the other hand, the metabolic turnover of PUFA may be slower than that of saturated fatty acids.

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Table 3. Linear regressions performed to estimate growth rates (k) of fish fed different rations.

Ration (% body weight·day^{-1})	Parameter estimate					
	k	c^a	r^2	F	df	P
1	0.040	−1.565	0.45	28.85	1,35	<0.0001
2	0.046	−1.556	0.40	28.24	1,42	<0.0001
3	0.051	−1.472	0.41	28.89	1,42	<0.0001
Pooled[b]	0.036	−1.319	0.27	40.48	1,111	<0.0001

[a]ln dry weight = k × sampling day + c.
[b]Fish on all three rations pooled together.

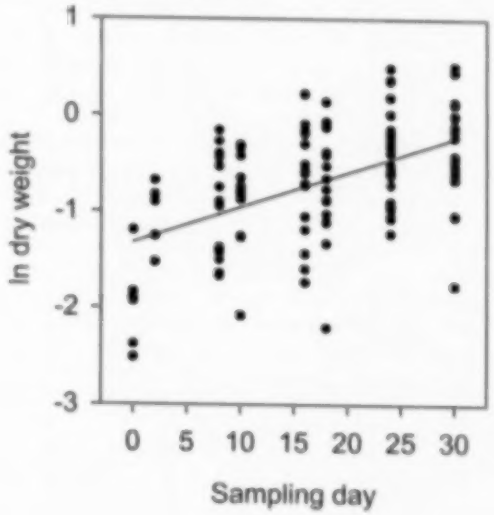
Table 4. Results of two-tailed t tests comparing growth rate estimates (k) (Table 3) of fish fed different rations.

Ration (% body weight·day^{-1})	t	df	P
1 vs. 2	0.586	75	>0.05
1 vs. 3	0.927	75	>0.05
2 vs. 3	0.344	82	>0.05

Although of no value in itself, the negative metabolic rate estimates may be combined with the growth rate estimate to give the overall rate of incorporation. The slower uptake of palmitic acid than of α-linolenic acid is consistent with the hypothesis that short-chain, saturated fatty acids are used predominantly for metabolic purposes, whereas PUFA are destined largely for structural growth. This may also explain the larger scatter observed in α-linolenic acid than in palmitic acid, i.e., the uptake of labelled α-linolenic acid reflecting the growth patterns of individual fish. Because of restrictions with the analytical equipment, we were unfortunately not able to measure the incorporation of labelled fatty acids into different lipid classes, and we were not able to measure growth in terms of lipid class composition, which could have consolidated the hypothesis.

The overall rates of incorporation of the two labelled fatty acids are not directly comparable, as the fish ingested approximately 16 times more palmitic acid than α-linolenic acid. On the other hand, such differences are presumably similar to what the fish encounter in the field and the uptake rates therefore more representative than if the fish were fed equal amounts of the two fatty acids. Another, more pertinent issue is that palmitic acid was fed as triacylglycerol, whereas α-linolenic acid was fed as methyl ester. The latter is not a natural food for fish, and experimental evidence with Atlantic salmon (*Salmo salar*) smolts has shown that fatty acids fed as ethyl esters are significantly less well absorbed than when fed as triacylglycerol or free fatty acid (Sigurgisladottir et al. 1992). This probably also applies to methyl esters, and hence, the estimated uptake of α-linolenic acid in this study is likely a conservative measure based on this issue as well as the effects of differential feeding. Addressing the latter issue, the estimated uptake rates, when modelling the top 25% of the population with respect to observed tracer levels, probably represent more realistic measurements. These "adjusted" uptake rates corresponded to a doubling time of 20 days for α-linolenic acid and 81 days for palmitic acid. In comparison, St. John and Lund (1996) found that

Fig. 2. Least squares regression (ln dry weight = −1.319 + 0.036 × sampling day; $F_{[1,111]} = 40.48$, $P < 0.0001$, $r^2 = 0.27$) of logarithmically transformed dry weights versus time of fish fed different rations pooled together.



the level of the specific diatom tracer 16:1(n − 7)/16:0 in first-feeding larval Atlantic cod (*Gadus morhua*) mirrored the ratio at the base of the food web within 13 days of feeding. Consistent with this, Weber et al. (2003) found that 18:1 is incorporated preferentially to 16:0 in storage lipids in rainbow trout, while both fatty acids enter tissue phospholipids to the same extent. Furthermore, Kirsch et al. (1998) demonstrated that the whole fatty acid signature of adult cod changed significantly towards their prey within 3–5 weeks of feeding. Hence, uptake rates of fatty acid tracers clearly depend on their physiological role, determined by their degree of unsaturation. In addition, the uptake rates are probably size and species specific, changing with the ontogenetic development and presumably also with the nutritional condition of the organisms.

In conclusion, this study demonstrates that stable carbon isotope labelled fatty acids can be used to document the incorporation of specific fatty acid tracers in fish, assess their uptake and clearance rate, and estimate their metabolic turnover rate. The incorporation of fatty acid biomarkers depends on their metabolic and structural role. Hence, whereas the uptake of labelled α-linolenic acid is driven largely by growth, the majority of labelled palmitic acid is probably

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Fig. 3. Observed (solid circles) and predicted (*a*) uptake of ^{13}C16:0, (*b*) clearance of ^{13}C16:0, and (*c*) uptake of ^{13}C18:3(*n* – 3) in the experimental fish. The predicted trends are modelled using a growth rate (*k*) of 0.0362·day^{-1} and fitting different levels of fatty acid metabolism (*m*). Dashed-dotted lines, mean control fish; triangles, *m* = 0; open circles, *m* = –0.032 (Fig. 3*a*), *m* = 0.020 (Fig. 3*b*), and *m* = –0.17 (Fig. 3*c*).

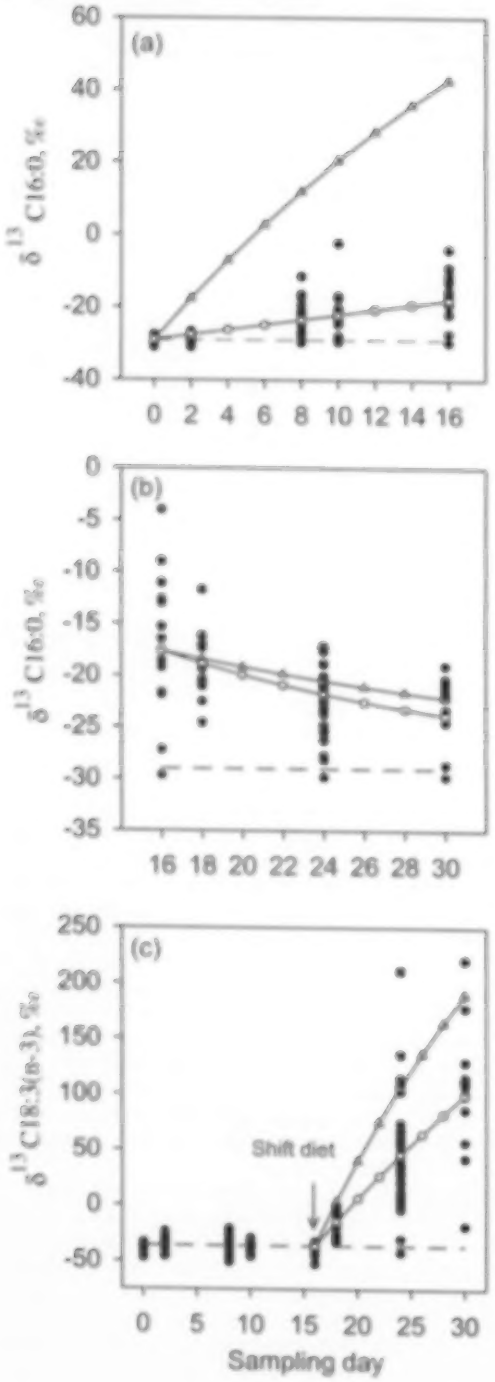
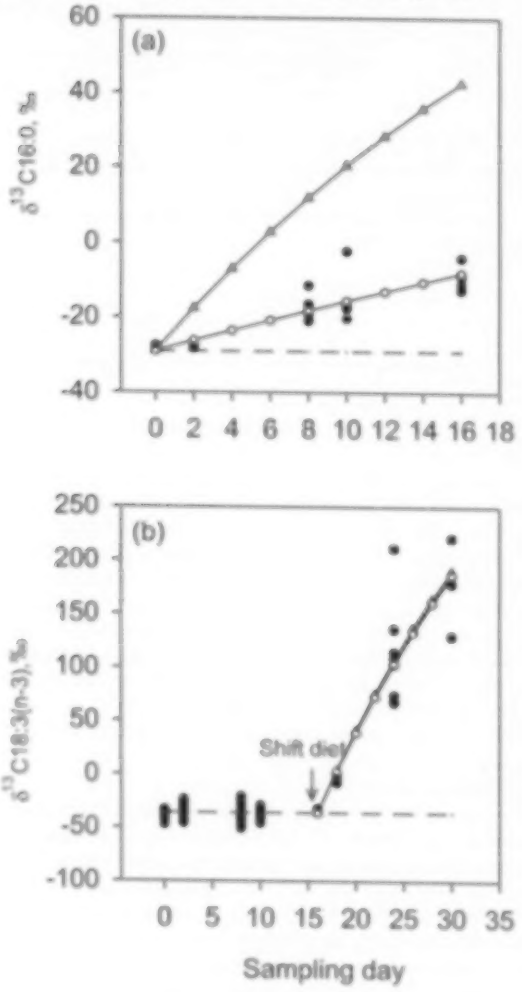


Fig. 4. Observed (solid circles) and predicted uptake of (*a*) ^{13}C16:0 and (*b*) ^{13}C18:3(*n* – 3) considering only the top 25% (with respect to observed tracer levels) of the experimental population. The predicted trends are modelled using a growth rate (*k*) of 0.0362·day^{-1} and fitting different levels of fatty acid metabolism (*m*). Dashed-dotted lines, mean control fish; triangles, *m* = 0; open circles, *m* = –0.0275 (Fig. 4*a*) and *m* = –0.0008 (Fig. 4*b*).



metabolized upon consumption or, alternatively, is not assimilated at all. Assuming that labelled α-linolenic acid and palmitic acid are representative of (*n* – 3) PUFA and saturated fatty acids, respectively, the results suggest that (*n* – 3) PUFA are "better" tracers than saturated fatty acids in actively growing, juvenile sandeel, integrating over a shorter feeding period. Compared with the uptake rate of palmitic acid, corresponding to a doubling time of 81 days, the clearance rate was much faster, with a half-life of only 12 days.

The implications of this study for future food web studies are highly significant. First, the study clearly identifies that fatty acid tracers can be used to identify key trophic interactions in marine food webs, consistent with the findings of St. John and Lund (1996) and adding to the body of litera-

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Table 5. Model output: estimated rates of fatty acid metabolic turnover (m) resulting in the best fit of the exponential model to the observed levels of labelled fatty acids in the fish.

Modelled period	Modelled part	k^a	m	$k + m^b$	r^2	Doubling time (days)
^{13}C16:0 uptake	Whole population	0.0362	–0.0321	0.0041	0.444	160
	Top 25% of population	0.0362	–0.0276	0.0086	0.79	81
^{13}C18:3(n – 3) uptake	Whole population	0.0362	–0.0165	0.0197	0.575	35
	Top 25% of population	0.0362	–0.0008	0.0353	0.830	20
^{13}C16:0 clearance	Whole population	0.0362	0.0211	0.0572	0.192	12[c]

[a]Growth rate.
[b]Overall uptake or clearance rates of labelled fatty acids.
[c]Half-life.

Table 6. Delta values (mean ± SD, n = 61) of nonlabelled fatty acids identified in the fish at the start, middle, and end of the experiment.

Fatty acid	Start experiment	Shift diet	End experiment
C14:0	–28.9±0.4	–28.7±1.0	–28.0±0.5
C16:1(n – 9)	–29.6±1.0	–30.0±2.7	–28.3±0.9
C18:0	–28.7±1.2	–27.0±1.3	–26.6±0.9
C18:1(n – 9)	–30.9±1.8	–30.6±1.8	–29.8±2.3
C18:2(n – 6)	–34.3±0.3	–39.0±4.7	–34.9±1.0
C20:1(n – 11)	–30.9±1.2	–30.7±1.5	–28.9±3.6
C20:4(n – 6)	–27.3±0.7	–28.9±1.7	–27.6±0.9
C20:5(n – 3)	–29.7±0.6	–31.0±1.8	–29.6±0.5
C22:6(n – 3)	–29.8±0.7	–30.0±1.4	–28.9±0.3

ture validating the utility of these tracers over a number of trophic levels and species. These findings strengthen the applicability of fatty acid tracers for identifying key trophic players to be used in the parameterization of predictive ecosystem models. Second, the study for the first time identifies the potential loss or depletion rates of fatty acid tracers relative to growth and metabolism, giving an estimate of the temporal window of utilization. It should be noted, however, that the estimated incorporation rates were heavily influenced by the feeding dynamics of the experimental population. It was clear that not all fish were fully utilizing the diet presented, and the results should therefore be viewed as conservative estimates of the incorporation rates. The estimated uptake rates obtained when modelling the top 25% of the population are presumably more in line with the activities of individuals feeding at more "optimal" rates. Our estimated depletion rate, on the other hand, is not as heavily dependent on feeding activity and hence is probably a representative estimation of the temporal dynamics of depletion.

Unfortunately, as outlined, for example, by St. John and Lund (1996) and Dalsgaard et al. (2003), fatty acid tracers employed independently of other measures cannot be applied in a quantitative manner, as it cannot be determined whether they are being incorporated or depleted. The present study, however, does aid in defining the temporal window over which fatty acid biomarkers integrate. Hence, implemented in future studies with a suite of other indices such as growth and condition, fatty acid tracers may become an important tool for identifying and eventually parameterizing the dynamics of key trophic interactions in marine food webs, necessary for developing predictive ecosystem models.

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Recovery of the South American sea lion (*Otaria flavescens*) population in northern Patagonia

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Abstract: The size of and trend in the South American sea lion (*Otaria flavescens*) population located in northern Patagonia were estimated and changes in the distribution, size, and structure of individual sites were analyzed during the period 1983–2002. Total counts were made during the reproductive season. Regression models were used to analyze the trend. Pups represented around 40% of the animals counted. The annual rates of change for pups and nonpups were not significantly different ($p > 0.05$, $n = 7$), although some rookeries showed higher rates of change for pups than for nonpups. Pup numbers have been increasing at the rate of 3.4% per year at the oldest rookeries, but the rate of increase was higher at new rookeries. Using Bayes' methods, the precision of the estimates and the contribution to the abundance of each rookery produced an alternative estimate of the trend in pup numbers in 5.7%. The key in the recovery of this population includes higher survival rates of juveniles combined with increased available habitat for newly reproducing individuals. This process led to the occupancy of new areas for hauling out and breeding. This hypothesis could explain the higher rates of increase in pups in peripheral areas while reproductive rates remain unchanged.

Résumé : Nous avons estimé la taille et la tendance de la population du lion de mer d'Amérique du Sud (*Otaria flavescens*) du nord de la Patagonie et nous avons analysé les changements dans la répartition, la taille et la structure des sites individuels de 1983 à 2002. Nous avons fait des dénombrements complets durant la saison de reproduction. Des modèles de régression ont permis d'analyser la tendance. Les petits représentent environ 40 % des animaux dénombrés. Les taux annuels de changement pour les petits et les autres lions de mer ne diffèrent pas significativement ($p > 0,05$, $n = 7$), bien que dans certaines échouries les taux de changements sont plus élevés pour les petits que pour les autres. Le nombre de petits augmente au taux de 3,4 % par année dans les échouries les plus anciennes et le taux est encore plus élevé dans les nouvelles échoueries. Au moyen de méthodes bayésiennes, la précision des estimations et la contribution de chaque échouerie à l'abondance ont généré une nouvelle estimation de la tendance dans le nombre de petits de l'ordre de 5,7 %. Le facteur essentiel de la récupération de cette population est un taux de survie plus élevé des jeunes combiné à la disponibilité d'habitats pour les individus qui débutent leur reproduction. Ce processus a eu comme conséquence l'occupation de nouveaux sites pour l'échouage et la reproduction. Cette hypothèse pourrait expliquer les taux plus élevés d'accroissement des petits dans les zones périphériques, alors que les taux de reproduction demeurent inchangés.

[Traduit par la Rédaction]

Introduction

South American sea lions (*Otaria flavescens*) are distributed along the whole Argentine coast on the southwestern Atlantic Ocean. More than 85 colonies located on the mainland and islands are known (Dans et al. 1996; Reyes et al. 1999; Schiavini et al. 1999). These colonies may represent breeding areas or rookeries during the reproductive season as well as haul-out sites where no reproductive activities take place. There is evidence of seasonal movements of animals between colonies at least in northern Patagonia (41–43°S) (Ximénez 1976; Lewis and Ximénez 1983). The population was heavily exploited during the first half of the twentieth century and protected during the 1970s. Currently, it is increasing slowly (Crespo and Pedraza 1991). In 1938, the number of sea lions in northern Patagonia was estimated at 137 500 (Godoy 1963), falling to almost 18 000 by 1946 (Carrara 1952). In southern locations (islands off Chubut, 45°S), where exploitation could have been more limited, the current number still represents one half of the number counted in 1952 (Reyes et al. 1999).

Colonies located in northern Patagonia were the most heavily exploited (Crespo and Pedraza 1991). Almost half of the skins exported from Argentina during the period 1930–

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1960 came from four rookeries located in this region (201 259 from a total of 493 438 skins). These colonies were also the best monitored since 1972. They did not show signs of recovery until 1990, when the number of pups born in the four main rookeries showed a positive annual rate of increase of 1.3% (Crespo and Pedraza 1991). The relatively slow increase and the delay in the recovery were interpreted at that moment as a consequence of sea lion demographics such as their naturally low intrinsic rate of increase.

As an alternative, the population's slow recovery has also been attributed to changes in environmental conditions (e.g., carrying capacity). Soon after the commercial exploitation ceased, the Patagonian high-seas fishery began to be developed and became very important in the 1980s. This may represent the major change that took place in this marine ecosystem and could have produced changes in the community and potential competitive effects on sea lions (Crespo et al. 1997; Koen Alonso et al. 2000).

At that moment, small breeding areas appeared within haul-out sites, where the arrival of presumably young adult males in juveniles areas was observed in previous years (Crespo 1988). This observation pointed out the dynamic nature of colonies and the transformation from haul-out to rookery as one of the potential mechanisms related to the recovery of this population. The expansion of areas used and the increase in the number of breeding sites would also be related to changes in vital rates.

Changes like those described above have been observed in other declining otariid populations as a way to investigate possible causes and consequences of the decline. Some studies suggest that resources other than food availability are important factors determining the expansion of colonies (York et al. 1996; Raum-Suryan et al. 2002). Therefore, studies of other otariid populations recovering after an important reduction may be helpful in better understanding patterns and processes involved in the recovery.

The objectives of this paper were to (*i*) analyze changes in the size, distribution, and structure of individual colonies of the South American sea lion in northern Patagonia, (*ii*) estimate the size of and trend in the population, and (*iii*) identify possible changes in the structure of the population.

Materials and methods

Study area

This study included the colonies located along the Argentine coast between Punta Bermeja and Punta León (Fig. 1). Censuses were carried out during the periods 1983–1987, 1989–1990, and 1993–2002, but the same colonies were not included in all surveys. A database for the periods 1972–1975 and 1982–1983 was also analyzed (Ximénez 1976; Castello et al. 1982; Lewis and Ximénez 1983).

Counting methodology

Total counts were made at the end of the reproductive season (mainly between the last week of January and first week of February), when most of the individuals are present at the rookeries for reproduction, and almost all of the pups were already born. In most cases, the counts were made from land and from elevated points when possible. On a few occasions (Barrancas Blancas in 1995 and Islote Lobos in 1994, 1995, and 1996), photographs were taken from a high-wing airplane (Cessna B182) and then counts were made from the photographs. However, these counts were not used in the population trend estimate. At least two counts were made both in the field and from the aerial photographs, with a maximum error of 10% allowed between them. The final value was estimated by averaging the selected counts, while those counts falling out of the fixed error were discarded.

Individuals were counted by age and sex: adult males, subadult males, females in breeding areas (both adult and subadult), juveniles mostly of unknown sex out of breeding areas (including yearlings born during the previous season), and pups (born during the season). These categories were based on body shape and color, location in the rookery, and behavioral cues. The number of animals in each category was counted separately. The total number of animals in each colony was calculated by summing the number counted in each age- and sex-class.

Number and age-class composition of colonies

Numerical models (e.g., regressions, general linear models, and general additive models) can be developed to adjust counts for environmental (tide height, time of day, sea state, and lunar phase) and survey-related effects (Link and Sauer 1997; Calkins et al. 1999; Frost et al. 1999). These models can increase accuracy in estimating and power in detecting population trends by reducing variability in counts (Hastings and Sydeman 2002). However, in this study, surveys were designed to count as many colonies as simultaneously as possible. Thus, it was not possible to survey a colony more than once, and as a result, within-season variability could not be analyzed, precluding the use of such models. However, censuses were carried out during the same fixed time window each year, reducing possible seasonal variations and expecting that during this window, most of animals are ashore. Also, most of the censuses were done in low-tide conditions because beaches are inaccessible otherwise. It is expected that the number of pups will not be affected by availability factors because they are constrained to stay at the rookery. Parturient and postpartum females are constrained to coming back to the same rookery, so the bulk of adult females is available during the surveys. However, other age-classes and particularly juveniles will be highly affected by environmental factors, leading to a higher dispersion of data.

The trend in each colony was analyzed by regressing the logarithm of the number of pups and nonpups on the year of the census. Only two classes were used in this analysis largely because of the variability in the classes that comprise the nonpup group. In several rookeries, it was possible to distinguish females from other classes, although it was not possible in colonies where juveniles were also present. Pups were more constrained to the rookery during the period of time when censuses were made, and as a result, the availability bias in the counts is minimal. Counts of nonpups, on the other hand, are subject both to bias (because of the different availability of age- and sex-classes during the surveys) and to errors resulting from misclassification to class (e.g., adult females and juvenile males appear similar). Because the number of adult males present can also be estimated with minimal error and bias, the relationship between pups and

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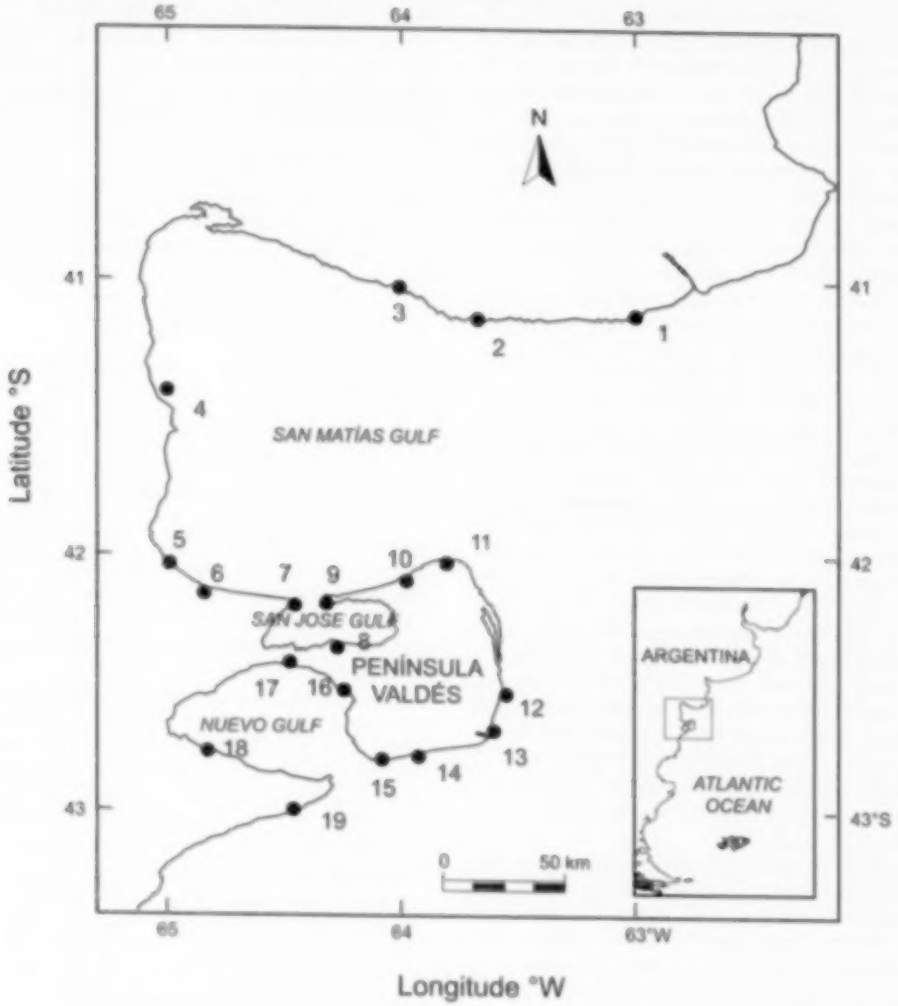
Fig. 1. South American sea lion rookeries and haul-out sites during the reproductive season (January–February) in northern Patagonia. 1, Punta Bermeja; 2, Faro Belén; 3, Caleta de los Loros; 4, Islote Lobos; 5, Rincon de Elizalde; 6, Barrancas Blancas; 7, Punta Quiroga; 8, Larralde; 9, Punta Buenos Aires; 10, La Armonia; 11, Punta Norte; 12, Punta Hércules; 13, Punta Delgada; 14, La Pastosa; 15, Morro Nuevo; 16, Punta Pirámide; 17, Las Charas; 18, Punta Loma; 19, Punta León.



adult males was also analyzed. The number of adult males present in the rookery is affected by the number of females still in oestrus, so that their numbers peak and then fall along the reproductive season. Crespo (1988) estimated that the number of males in the breeding area peaks on 20 January and then falls to 75% of this around 31 January. Therefore, three periods were considered for analyzing the number of pups per adult male: before 20 January, between 20 and 31 January, and February.

Differences between slopes for pups and nonpups in each individual site were evaluated by F tests. Overall differences among trends in the number of pups and nonpups in all rookeries were compared by F tests, and all possible pairs of slopes were compared by Tukey–Kramer, T', and GT2 tests (Sokal and Rohlf 1995; Zar 1996). Assumptions of the regression model were verified by visual inspection of residuals.

The historical information collected during the last three decades on each rookery or haul-out was analyzed to further review the changes that had occurred. This information is mostly descriptive and is reported for each specific individual site. Spatial and age-class composition changes in the old or new individual rookeries were reviewed to describe the recolonization pattern.

Population size, trend, and structure

The present population size for northern Patagonia was estimated from counts made in 19 colonies during 2001 and 2002. The very wide area to be surveyed over a short time presented particular problems in providing a population estimate. Then, not all the colonies could be counted each year, sometimes for logistical reasons or because of bad weather conditions. Therefore, counts made in different colonies and

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years must be combined. Colonies 8–17 and 19 were surveyed in 2001, while colonies 2–7 and 18 were surveyed in 2002. Although rookery 1 was surveyed in 2002, the census was discarded because of bad weather conditions, and the census carried out in 2000 was considered.

Censuses, even if conducted during the reproductive season, may underestimate the population size because an unknown proportion of animals are at sea; this may include the juvenile component of the population. To estimate total population size, it is necessary to develop and apply a correction factor to account for the animals missed. One approach is that used by Crespo (1988) who developed life tables for this population utilizing the age structure at death assuming a stationary population. Then, from a known number of pups born (l0 in the life table) and the survivorship schedule, Crespo (1988) estimated the total number of sea lions. The factor was calculated as the ratio between estimated (E) and counted (C) numbers (17 804 and 9834, respectively; Crespo 1988) being $E/C = 1.8$, which means that close to 45% of the animals are not present in the surveys.

Possible changes in the population structure were explored by comparing rates of annual change in different age-classes. These analyses were performed considering eight colonies, which represent around 70% of the total number and 80% of the total of pups counted between 2000 and 2002. These eight colonies included the historical four main rookeries Punta Buenos Aires, Punta Norte, Punta Pirámide, and Punta León (sites 9, 11, 16, and 19 in Fig. 1) as well as colonies at Punta Bermeja, Punta Quiroga, Punta Hércules, and Punta Delgada (sites 1, 7, 12, and 13 in Fig. 1). The following groups were analyzed: pups and nonpups (all age- and sex-classes pooled), juveniles, adult females, adult males, and subadult males. Rates of change were estimated by regressing the logarithm of the number of individuals counted in each class on the year of the census (Caughley 1977) and assumptions of the regression model were verified by visual inspection of residuals.

Population trajectory was estimated in two ways. One way was to regress the logarithm of the total population at key colonies on time (summation of the number of pups and nonpups in all colonies each year). For this analysis, the eight colonies mentioned above were selected because they were surveyed at the same time in the same year. Data for the periods 1972–1975 and 1981–1983 were available, but they only included pup counts at the four main rookeries (Ximénez 1976; Lewis and Ximénez 1983). A second approach was to calculate a weighted average of the trends in individual colonies (Calkins et al. 1999). Each trend was adjusted by the precision of the estimate and the contribution of each colony to the population size. Only colonies with enough information for the period 1983–2001 were considered. This calculation was done following Calkins et al. (1999), who adjusted each trend and its variance by empirical Bayes' methods. For each site, we computed the Bayes weight wt_b as

$$wt_b = vt/(vt + \tau^2)$$

where vt is the variance in the trend estimate, $\tau^2 = Vt - vt_{mean}$, Vt is the variance among all trends estimates, and vt_{mean} is the mean of all of the variances. Then, the trend estimate as well as its variance were adjusted as

$$t_b = (t_{mean} wt_b) + [t(1 - wt_b)]$$

$$vt_b = wt_b \tau^2$$

where t_b and vt_b are the trend and its variance adjusted and t_{mean} is the mean of the estimated trends.

For each rookery, we computed the mean contribution to the total number of pups as the average of the abundance weight wt_A along the years. We computed the weight wt_A for each rookery for each year as

$$wt_A = C/\sum C$$

where C is the count of pups in each rookery.

Then, the trend and its variance adjusted by Bayes for the precision were readjusted by the mean abundance weight as

$$t_{b\text{-}A} = \sum(\overline{wt}_A t_b)$$

$$vt_{b\text{-}A} = \sum(\overline{wt}_A^2 vt_b)$$

Results

Trend of major rookeries

During the reproductive seasons of 2001 and 2002, South American sea lions were present at least at 19 colonies. Breeding activities were recorded in almost all of them by the end of the study (Table 1). The four main rookeries were Buenos Aires, Norte, Pirámide, and León and the less important sites at Islote Lobos and La Armonía. Buenos Aires, Norte, and León represented the most important breeding areas in northern Patagonia, accounting for almost 60% of the total number of pups born in 2001.

All of these rookeries showed positive trends in the number of pups as well as in the number of nonpups (Table 2). Some remarkable changes were found at León. This rookery showed a higher rate of increase in the number of pups than in the number of nonpups ($p < 0.05$) (Table 2). At the same time, there was an increase in the extension of the beach occupied each year. Several small groups began to appear southwards each year 1.5–2 km away from the main breeding area. These small groups were mostly juveniles but also included a few females with pups. In 1994, this area of the colony included 96 pups out of a count of 510 individuals (18%). In 2001, the last year of census, there were 240 pups and a total of 651 individuals (36%).

Pirámide was another important breeding area during the first years of the study. However, it only included 8% of the total number born in 2001–2002. The trend in the number of nonpups in this rookery was not significant (Table 2).

In all of these rookeries, the number of pups per adult male seemed to be constant along the study period, being 5.92 (SE = 2.19), 5.21 (SE = 1.18), and 5.71 (SE = 2.61) in Buenos Aires, León, and Pirámide, respectively, while in Norte the ratio was 3.91 (SE = 0.95).

Trend in juvenile aggregations and haul-out sites

Only 3 out of 19 colonies included exclusively juveniles or nonbreeding animals during the whole study period. These colonies were Caleta de los Loros, Hércules, and La Pastosa (Table 1) and included mostly juveniles of both sexes and subadult males. Caleta de los Loros showed a positive trend equal to 11.3% ($p < 0.05$) (Table 2). Although Caleta de los Loros was described as a haul-out during most of the study,

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Table 1. Brief history of South American sea lion haul-out sites and rookeries in northern Patagonia between 1970 and 2002.

Location	Description before this study	First census			Last census		
		Year	Pups	Nonpups	Year	Pups	Nonpups
Bermeja	Not available	1982	30	620	2000	480	2356
Belén	Not available	1995	9	403	2002	160	849
Caleta de Los Loros	Not available	1982	0	150[a]	2002	16	514
Islote Lobos	Rookery[b]	1990	167	464	2002	693	1164
Rincón de Elizalde	Not available	1996	4	451	2002	8	64
Barrancas Blancas	Not available	1995	135	484	2002	509	476
Quiroga	45–70 adult and subadult males[c]	1983	88	233	2002	462	567
Larralde	Not available	Not available			2001	41	190
Buenos Aires	Rookery[c]	1983	957	729	2001	1778	1271
La Armonía	Not available	1990	116	230	2001	510	365
Norte	Rookery[c]	1983	941	910	2001	1975	2243
Hércules	Adult males[c]	1983	0	175	2001	0	122
Delgada	Subadult males and juveniles[c]	1983	0	757	2000	48	1289
La Pastosa	Juveniles[d]	1996	1	1757	2001	2	847
Morro Nuevo	Juveniles[c]	1987	3	477	2001	895	651
Pirámide	Rookery[c]	1983	506	573	2001	824	525
Las Charas	Not available	1998	48	282	2001	45	280
Loma	Juveniles[c]	1986	4	86	2002	52	436
León	Rookery[c]	1983	737	942	2001	1570	1642

Note: Data for between 1983 and 2002 come from this study. Data before this period were available from the literature.
[a]This census was done on 28 March.
[b]Castello et al. (1982).
[c]Monitored during 1972–1974 (Ximénez 1976).
[d]Possibly wintering haul-out referenced as Pico Lobo by Ximénez (1976).

Table 2. Trends in pups and nonpups of South American sea lion haul-out sites and rookeries in northern Patagonia during the period 1983–2002.

Rookery	Pups				Nonpups				
	n	Slope	95% CI[a]	*p*	*n*	Slope	95% CI[a]	*p*	*F* test *p*[b]
Bermeja	8	0.131	0.076; 0.186	0.001	8	0.069	0.007; 0.130	0.035	0.341
Caleta de los Loros	No pups				7	0.113	0.031; 0.195	0.001	
Quiroga	13	0.088	0.057; 0.119	<0.001	12	0.054	0.030; 0.078	<0.001	0.040
Buenos Aires	13	0.043	0.025; 0.060	<0.001	13	0.033	0.020; 0.046	<0.001	0.340
La Armonía	7	0.140	0.067; 0.213	0.002	7	0.044	–0.080; 0.168	0.314	
Norte	15	0.040	0.027; 0.053	<0.001	15	0.056	0.036; 0.076	<0.001	0.120
Hércules	No pups				13	0.054	–0.070; 0.178	0.362	
Delgada	9	0.233	0.142; 0.324	<0.001	12	0.014	–0.019; 0.048	0.289	
La Pastosa	No pups				6	–0.107	–0.295; –0.081	0.190	
Morro Nuevo	8	0.376	0.207; 0.546	<0.001	8	0.040	–0.036; 0.116	0.170	
Pirámide	14	0.025	0.012; 0.039	0.002	14	0.017	–0.004; 0.038	0.059	
Loma	10	0.151	0.092; 0.210	<0.001	11	0.117	0.059; 0.174	<0.001	0.290
León	14	0.042	0.029; 0.055	<0.001	14	0.025	0.012; 0.037	0.001	0.042

[a]Confidence interval.
[b]*F* test for differences among slopes of pups and nonpups.

three adult males and 16 pups were observed there in 2002. Hércules showed large yearly variations with no trend. La Pastosa was first studied in 1996 and there is not enough information to evaluate its trend. Nevertheless, this site represented an important reservoir of nonbreeding individuals, fluctuating between 700 and 1700 animals counted there during 1996–2001.

Trend and changes in newly developed breeding areas

The remaining sites presented a mixed structure of breeding areas with a large number of juveniles or nonreproductive animals in close proximity. Other sites were small aggregations with few births during the first years of the study but became breeding areas during the study period.

Quiroga and Morro Nuevo represented the most important new rookeries that have evolved from haul-out sites (Table 1). Previous information about Quiroga indicated the presence of subadult males only (Ximenez 1976). By 1983, this colony was mainly composed of juveniles with a small breeding area, with 88 pups. The percentage of pups increased thereafter reaching close to 50% of the total number by 2001. Although both pups and nonpups showed positive

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trends, pup numbers increased at a higher rate (Table 2). The pups to adult male ratio was 7.10 (SE = 3.26). Morro Nuevo only contained nonbreeding age-classes and no reproductive events took place during the 1980s (In 1987, only three pups were found at this site). However, by 1995, 50% of the population at this site were pups. The trend in the number of pups was positive, while no trend was observed in nonpup numbers (Table 2).

Bermeja, Delgada, and Loma are important reservoirs of juveniles. They presented small breeding areas in constant growth, although the nonbreeding fraction still represents more than 80% of the total number (Table 1). Both pups and nonpups increased at similar rates (Table 2), while the number of pups per adult male reminded at around 3.31 (SE = 0.81). Births were seen only sporadically at Delgada through 1992 (two or three pups in 1972–1975; Ximenez 1976). In 1992, a landslide made the animals move to an adjacent beach and a small group of adult males, females, and pups appeared in the original location. Here, the new breeding area was separated by 1.5 km from the juvenile haul-out.

The remaining sites Belén, Barrancas Blancas, Larralde, Las Charas, and Rincón de Elizalde were monitored after 1995 (Table 1). Even though there are few data for estimating their trends, they seemed to be increasing. Each colony was composed mostly of nonreproductive individuals with a small amount of breeding areas.

Comparison among individual sites

All rookeries showed significant trends in pup production. Different rookeries showed different trends in the number of pups as well as in the number of nonpups (Table 2). Pirámide showed the lowest rate of increase in the number of pups, but it was not statistically different from the other important and traditional breeding rookeries Norte, Buenos Aires, and León ($p > 0.05$). This rookery showed an increase of 2.5% per year in the number of pups. Less traditional breeding sites such as Bermeja, Quiroga, Loma, and La Armonía exhibited higher rates of increase. Although the breeding area is still small, Delgada showed a higher rate of increase and Morro Nuevo the highest among all rookeries, 37.6% per year (Tukey–Kramer and GT2, $p < 0.05$).

With respect to the nonpup fraction, Buenos Aires, León, and Pirámide showed the lowest significant trends, while Loma and Caleta de los Loros showed the highest (Tukey–Kramer and GT2, $p < 0.05$). One interesting result is that Morro Nuevo, Delgada, and La Armonía did not show significant trends in the number of nonpups (Table 2).

Population size, trend, and structure for northern Patagonia

The total number of individuals counted was 16 807 sea lions in colonies 8–17 and 19 in 2001, while 5269 sea lions were counted in colonies 2–7 and 18 in 2002 (Table 3). Although rookery 1 was surveyed in 2002, the census was discarded because of bad weather conditions, and the census carried out in 2000 was considered. Then, in 2001–2002, the total number of sea lions counted was 24 912 (Table 3). Then, applying a correction factor of 1.8, the population size in northern Patagonia was estimated to be 44 842 sea lions. Pups represented around 40% of the total counts, while they would represent 22% of the estimated population size.

Taking into account the data on the eight selected rookeries and haul-outs during the period 1983–2001, the proportion of pups in the population did not change (Fig. 2). Discriminating individuals in the other age-classes whenever possible, the female proportion seemed to remain constant, while the proportion of juveniles would be increasing (Fig. 2). Nonpups seemed to be increasing at a slightly higher rate than pups, but there were no significant differences between them ($p > 0.05$, $n = 7$) (Table 4). Juveniles showed the highest rate of increase, female numbers were increasing at the same rate as pup numbers, while adult and subadult males did not show significant trends (Table 4). The population at these selected colonies increased by 4.3% per year for the period 1983–2000. The ratio of pups per adult male averaged over all of the rookeries during all of the surveyed years did not show a clear pattern of change ($p > 0.05$). Although highly variable among rookeries, the ratio appears to remain constant through time with a mean of 5.52 pups per male during the time window considered here (21–31 January of each year) (Fig. 3).

Assuming that pups and nonpups would be increasing at the same rate, the population trend may be estimated from the trend in the number of pups. The trend observed in the eight selected colonies was estimated to be 3.9% annually for the period 1983–2000. Considering only the four major rookeries, the trend was estimated to be 3.4% for the same period 1983–2000, and including available data for the period 1970–1980, the trend is still positive but lower (2.9%) ($p < 0.001$) (Fig. 4).

The trend estimated by the weighted average is markedly higher than the trend estimated for the eight selected sites and even more considering only the four major rookeries for the same period 1983–2000 (Fig. 4). Considering the precision and contribution to the abundance of each rookery, the weighted average trend in the number of pups was estimated to be 5.7% (Table 5).

Discussion

There is clear evidence that the South American sea lion population in northern Patagonia is steadily increasing. Although a slight increase was detected in the early 1990s, the population increased at a rate close to 5.7% annually during the period 1983–2002. As a result, the population status has almost doubled since the beginning of the study period. This still represents less than a quarter of the original population's estimated size prior to the highest levels of exploitation (Crespo and Pedraza 1991).

This work also contributes to the knowledge of possible values of annual rates of increase for an otariid population after it was dramatically reduced by exploitation. The abundance levels that this South American sea lion population reached were very low considering that it was reduced to less than 10% of the original size. The observed rate could therefore be interpreted as being very close to its maximum rate. This population is increasing at a relatively high rate and this result agrees with the suggestion that the reduction in population rate of increase at low densities in otariid populations may not be strong (Gerber and Hilborn 2001). However, this population would have low rates of increase when compared with other otariids, such as northern fur seal

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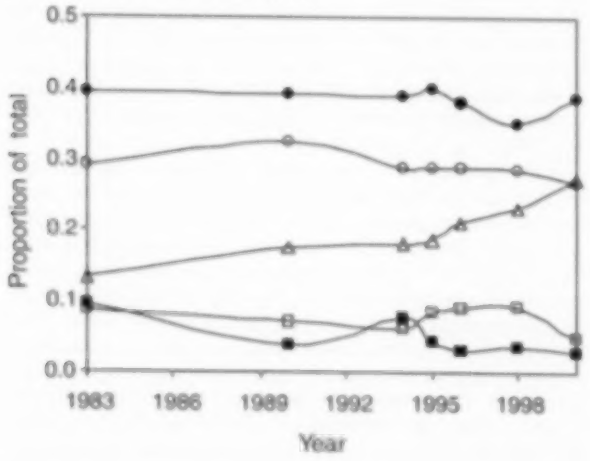
Table 3. South American sea lion counts in 19 colonies in northern Patagonia in 2000, 2001, and 2002.

Rookery	Date of census	Year of census	Adult males	Subadult males	Females	Juveniles	Pups	Total
1. Bermeja	5 Feb.	2000	23	35	378	1920	480	2 836
2. Belén	25 Jan.	2002	47	2	39	761	160	1 009
3. Caleta de los Loros	24 Jan.	2002	3	12	42	457	16	530
4. Islote Lobos	30 Jan.	2002	32	3	121	315	693	1 164
5. Elizalde	30 Jan.	2002	1	2	1	52	8	64
6. Barrancas Blancas	29 Jan.	2002	39	45	124	268	509	985
7. Quiroga	23 Jan.	2002	65	12	291	226	462	1 029
8. Larralde	7 Feb.	2001	1	4	0	185	41	231
9. Buenos Aires	29 Jan.	2001	175	59	953	84	1 778	3 049
10. La Armonía	29 Jan.	2001	61	2	288	14	510	875
11. Norte	30 Jan.	2001	305	158	1389	391	1 975	4 218
12. Hércules	30 Jan.	2001	0	40	0	82	0	122
13. Delgada	30 Jan.	2001	11	45	0	975	0	1 031
14. La Pastosa	2 Feb.	2001	4	33	0	810	2	849
15. Morro Nuevo	1 Feb.	2001	92	21	611	130	895	1 546
16. Pirámide	31 Jan.	2001	107	11	392	15	824	1 349
17. Las Charas	31 Jan.	2001	6	0	0	274	45	325
18. Loma	28 Jan.	2002	10	1	0	597	52	488
19. León	29 Jan.	2001	342	111	1058	131	1 570	3 212
Total			1324	596	5687	7687	10 020	24 912

Note: Counts for the different age-classes and total number in each colony are given.

Fig. 2. Proportion of South American sea lion individuals in each of the five age-classes considered in this study. The proportions were calculated on the total number of animals present in eight selected sites in seven different years. Open squares, adult males; solid squares, subadult males; triangles, juveniles; open circles, females; solid circles, pups.



(*Callorhinus ursinus*), and even more so when compared with species of the genus *Arctocephalus* (Wade 1998). Antartic fur seal (*Arctocephalus gazella*) pup counts on South Georgia showed a rate of increase of 16.8% between 1958 and 1972 (Payne 1977).

It is expected that the observed recovery is due to responses in demographic aspects such as survival and reproduction, without immigration from other sites, since all possible sources were also reduced and still recovering

Table 4. Trend in the South American sea lion population in northern Patagonia by age- and sex-class.

Age-class	Change (%)	95% CI	*p*
Pups	3.9	0.028; 0.05	<0.0001
Nonpups	4.6	0.029; 0.063	0.001
Females	3.8	0.020; 0.055	0.001
Juveniles	8.0	0.051; 0.113	<0.0001
Adult males	3.1	–0.180; 0.080	0.165
Subadult males	–1.9	–0.074; 0.035	0.404

Note: The figures used for this analysis represent the total number of individuals counted in eight selected rookeries and haul-out sites surveyed at the same time between 1983 and 2000 ($n = 7$). Counts were log-transformed. CI, confidence interval.

(Reyes et al. 1999). Possible changes in the structure of this population was also explored as one of the expected consequences of changes in survival and reproduction. The numbers of pups and nonpups are increasing at the same rate. However, among nonpups, juveniles showed the highest rate of annual change, suggesting that their proportion in the population is increasing.

The other noticeable result shown in this paper is that although most colonies presented positive trends, there was a great variability in the rate of change among them, at least in the number of pups in different rookeries. The trend in the number of pups in the major breeding areas during the period 1970–2000 was significantly positive but lower than that estimated for all of the rookeries during 1983–2000 (2.9% and 5.7%, respectively). More important is the fact that the highest rates of increase were seen at those sites that turned into rookeries during the period of the study or the ones that do not represent an important contribution to the total number of sea lions in this population. These higher

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Fig. 3. Relationship of the number of South American sea lion pups per adult male and the year of the census. Each datum represents the mean number among all of the rookeries from censuses after 20 January and before 31 January, and the broken line represents the mean number across the years.

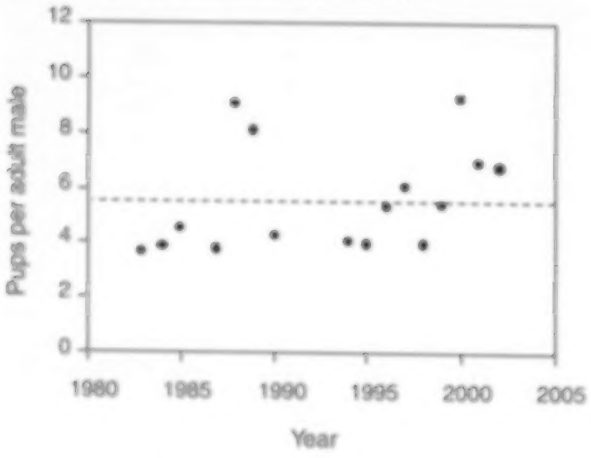
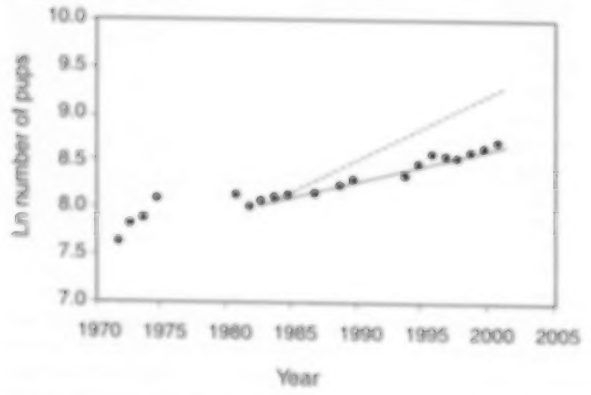


Fig. 4. Counts of South American sea lion pups in the four main rookeries between 1972 and 2000. The trend in these rookeries was estimated to be 3.4% increase per year for 1980–2000 (solid line), while the trend would be estimated to be 5.7% taking into account other rookeries and sites with newly developed breeding areas (broken line).



rates in marginal areas might be partially explained by their small size. However, along with this higher rate of increase, important changes in sea lion distribution were also observed, including the expansion of the original area occupied by a colony, a relocation of the whole colony, and changes in age-class composition. Therefore, aside from any potential bias and comparing with the main rookeries, it is clear that something different is occurring in these marginal areas.

Several factors may lead to recovery of pinniped populations. Demographic aspects with behavioral aspects such as pupping and the utilization of hauling sites for breeding can be interacting and affecting the potential of the population for recovering. The Steller sea lion (*Eumetopias jubatus*) in the north Pacific Ocean is perhaps the species that attracted more attention. York (1994) suggested that the survival of juveniles was the main factor affecting the population growth. Their stocks, as well as the sites within each one, showed different trends in abundance. While the western stock is still showing the most severe decline, the eastern stock has shown decreasing as well as increasing areas (York et al. 1996; Calkins et al. 1999). The relationship among the location of the breeding site and the foraging area was explored as a possible explanation of these differences. However, York et al. (1996) found that consistent groupings of rookeries with similar trends ranged from couplets of adjacent rookeries (within 37 km of each other) to groupings of five or more sites spread over several hundred kilometres. More recently, studies of dispersal and philopatry suggested that the dispersal of females to new rookeries, while the parent rookery remained stable in size, may have been a density-related response (Raum-Suryam et al. 2002). Aside from the differences in life history between otariids and phocids, a similar density-related pattern was also suggested for the increasing population of grey seals (*Halichoerus grypus*) in the United Kingdom, which showed old stable colonies as well as new colonies becoming established (Pomeroy et al. 2000*a*). One of the new colonies increased the area occupied instead of increasing the density in the existing breeding area (Pomeroy et al. 2000*b*). Gerrodette and Gilmartin (1990) suggested a process like this, although at a smaller scale, for Hawaiian monk seals (*Monachus schauinslandi*), remarking the importance of undisturbed beaches by humans.

The results in the present study suggest that the occupancy of new areas for hauling out as well as for breeding may represent the key to the recovery of South American sea lion population. The most important features in this process would be higher survival rates of juveniles combined with available habitat for individuals entering to reproduce and then establishing in new rookeries. This hypothesis could explain the higher rates of increase in the number of pups in the peripheral breeding groups and that the relationships such as pups per adult male remain unchanged. If this hypothesis is supported, the population would not be increasing without available and suitable new sites.

Such spatial and demographic changes when analyzed through time indicate that we are observing a dynamic process driven initially by juvenile animals occupying a new site. The continuing growth of the central breeding areas eventually leads to segregation of adults and pups in one area and juveniles in another. This expansion is promoted by density-dependent factors that limit the number of sea lions reproducing in the well established breeding areas and lead to the fission of the colony. Note that there is a subjective perception that males and females in these new formed breeding areas are smaller in size than those occupying territories in the traditional and old breeding areas. It is not possible to test this hypothesis with the present data but it represents an interesting point to explore in future studies.

As pups and nonpups showed similar trends, the annual rate of change in pups was used as an indirect measure of the population trend. On one side, pup counts may lead to more accurate estimates, since they are more constrained to the breeding site, and then the probability of being counted is high and not affected by environmental factors. However, pups are more susceptible to mortality catastrophic events, leading to years with lower pup production; this will give

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Table 5. Trends in the number of South American sea lion pups in each rookery (t) and population trend (t_{b-A}) and its variance (vt_{b-A}) adjusted by the precision of trend estimate and the contribution of each rookery to the total number of pups.

Rookery	t (%)	vt	wt_b	t_b	vt_b	Mean wt_A
1. Bermeja	13.114	5.0697	0.04264	13.0967	4.8536	0.0354
7. Quiroga	8.827	1.4359	0.01245	8.8749	1.4178	0.0436
9. Buenos Aires	4.262	0.6392	0.00558	4.3090	0.6356	0.2282
10. La Armonía	14.046	5.3089	0.04456	13.9858	5.0723	0.0267
11. Norte	3.998	0.3674	0.00322	4.0259	0.3662	0.2343
13. Delgada	23.344	10.2490	0.08260	22.4657	9.4024	0.0022
15. Morro Nuevo	37.621	32.5790	0.02225	32.0774	25.3298	0.0309
16. Pirámide	2.538	0.4090	0.00358	2.5748	0.4075	0.1335
18. Loma	15.108	4.6083	0.03891	15.0144	4.4290	0.0040
19. León	4.210	0.3375	0.00296	4.2346	0.3365	0.2612
t_{b-A}	5.7018					
vt_{b-A}	1.5636					

negative or no significant trend in the number of pups after some suboptimal years but not necessarily a negative trend in the population. Another factor that can bias the population trend estimate based on the rate of change of pups is the fact that density-dependent mechanisms may act before or after the time of the census, giving under- or overestimated rates of change (Berkson and DeMaster 1985). In this particular population, we do not expect that density-dependent mortality of pups may produce strong bias in the trend estimate.

Also, pups are a measure of the productivity of the population, and they provide a better index of population trend than do counts of nonpups (Trites and Larkin 1996). However, pups represent production, and they only add to the population if they survive. Then, if there are more pups being born, either female fecundity has gone up or pup to juvenile survival has been good previously, adding to the total number of females alive.

Most of the breeding sites showed higher rates of change in the number of pups than in the number of nonpups, while most of the haul-outs did not show significant trends. The existence of higher rates of increase in the number of pups in some rookeries, such as León and Morro Nuevo, seem to be associated with the sudden consolidation of new breeding areas in the periphery of the original colony. In addition, the relocation of juveniles to new sites away from the original one was observed. The pups born in the haul-outs that turned into rookeries still represent a low percentage of the total number of animals present in those sites. Also, as most of them are juveniles and nonbreeding individuals, there is a large fluctuation in the number present in the site at the moment of the census. Such variability precludes reliable estimates of the trend in the number of nonpups and the comparison with the trend in pups. In spite of this, it seems that the number of pups is increasing and the number of nonpups in each rookery or haul-out is also increasing.

In addition to possible explanations for the population increase in South American sea lions, this paper also provides implications for management purposes. Península Valdés is a protected area where the land belongs to private owners. The largest and traditional rookeries are protected by gamekeepers. On the other hand, most of the smaller and newly developed breeding sites with a higher rate of increase lack any protective measures, being subject to perturbations by local people, tourism, or illegal activities.

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Cage aquaculture and water-quality changes in the LaCloche Channel, Lake Huron, Canada: a paleolimnological assessment

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Abstract: Lake eutrophication due to cage aquaculture is an area of concern in Ontario; however, without knowledge of pre-impact conditions, it is difficult to determine the extent and magnitude of environmental change. Paleolimnological techniques were used to estimate water-quality conditions prior to, during, and briefly following aquaculture operation in the LaCloche Channel, Lake Huron. Past oxygen and nutrient levels were inferred from assemblages of chironomids and diatoms, respectively, to determine whether recent low-oxygen and nutrient-rich conditions were related to cage aquaculture in operation from 1989 to 1998. Chironomid assemblages exhibited trends consistent with decreased hypolimnetic oxygen levels, with reductions in oxic-type profundal taxa and increased relative abundances of littoral communities. Diatom assemblages reflected a period of nutrient enrichment by increased relative abundances of meso-eutrophic taxa. Improvements in water quality are inferred from assemblages of diatoms in surface sediments, which may correspond to the cessation of fish-farming activities in 1998. In contrast, no sign of deep-water oxygen recovery is recorded by chironomids. These trends are consistent with eutrophication, and suggest that the LaCloche Channel was sensitive to nutrient loading from the cage-aquaculture operation. This study demonstrates the potential of using paleolimnological techniques to track water-quality changes associated with cage farming.

Résumé : L'eutrophisation causée par l'aquaculture en cages est un problème préoccupant en Ontario; cependant, sans informations sur les conditions antérieures, il est difficile de déterminer l'étendue et l'importance des changements environnementaux. Nous avons utilisé des techniques paléolimnologiques pour évaluer les conditions de la qualité de l'eau avant, pendant et peu après une opération d'aquaculture dans le chenal LaCloche au lac Huron. Nous avons déduit les concentrations d'oxygène et de nutriments du passé de l'analyse respectivement des chironomidés et des diatomées afin de déterminer si les conditions récentes d'oxygène réduit et de nutriments élevés sont reliées aux activités d'aquaculture en cages qui y ont eu lieu de 1989 à 1998. Les communautés de chironomidés montrent des tendances qui sont compatibles avec une réduction de l'oxygène dans l'hypolimnion, avec une diminution des taxons oxybiontes de la région profonde et une augmentation de l'abondance relative des communautés littorales. Les communautés de diatomées indiquent une période d'enrichissement en nutriments par l'augmentation de l'abondance relative des taxons méso-eutrophes. Nous avons déduit l'existence d'une amélioration de la qualité de l'eau de l'analyse des diatomées des sédiments superficiels, amélioration qui peut correspondre à l'arrêt des activités de pisciculture en 1998. En revanche, nous ne trouvons aucune trace de récupération des conditions d'oxygène dans les eaux profondes à partir de l'examen des chironomidés. Ces tendances sont compatibles avec l'eutrophisation et laissent croire que le chenal LaCloche était sensible à l'apport des nutriments provoqué par les opérations d'aquaculture en cages. Notre étude démontre le potentiel de l'utilisation des techniques paléolimnologiques pour suivre les changements de la qualité de l'eau associés à l'élevage en cages.

[Traduit par la Rédaction]

Introduction

Intensive fish farming in lakes is a relatively new pressure on Canadian aquatic ecosystems. Although still regarded as a small industry in Canada, fish farming is rapidly expanding, particularly in Ontario, where cage production of rainbow trout (*Oncorhynchus mykiss*) has increased dramatically since the mid-1980s (Moccia et al. 1997). The Manitoulin Island – Georgian Bay area (Fig. 1) accounts for over 95% of cage production of rainbow trout in this province (Moccia et al. 1997) and consequently receives significant nutrient loadings from fish wastes (uneaten fish food and feces). Annual loadings in the North Channel of Lake Huron and Georgian Bay alone are estimated at 15 t of total phosphorus, 90 t of nitrogen, and 500 t of solid waste (Gale 1999*b*). Untreated wastes from these cage operations are discharged directly into the aquatic environment, and so there is grow-

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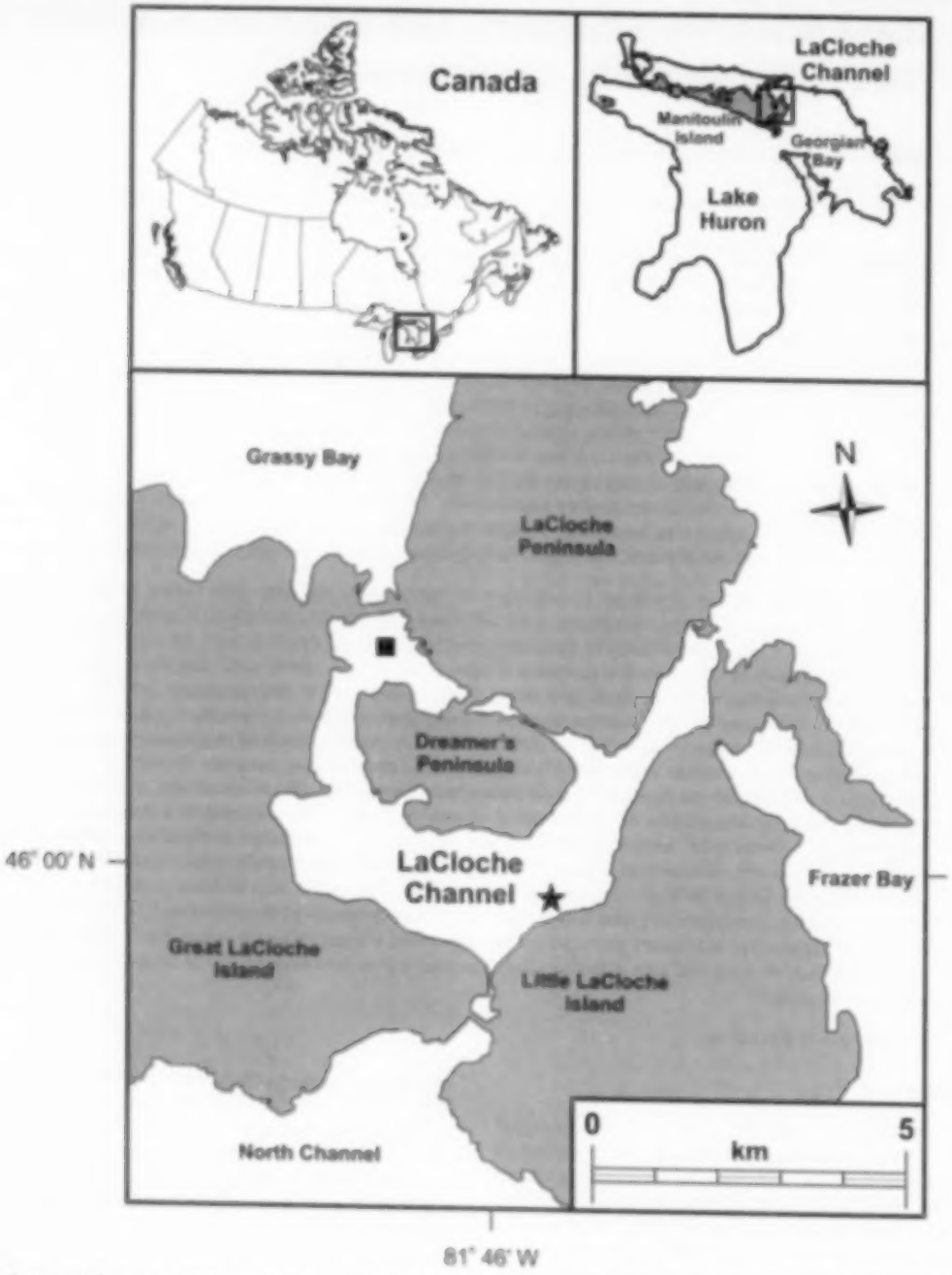
Fig. 1. Map of the North Channel of Lake Huron showing the location of the LaCloche Channel core site (★). The Ontario Ministry of Natural Resources site (■) was operational from 1985 to 1992.



ing concern that cage farming poses a serious eutrophication risk.

In the Great Lakes, only one study to date has examined water-quality impacts from cage aquaculture (Hamblin and Gale 2002), despite the importance of this area for large-scale aquaculture operations. This reflects the fact that most aquaculture research in Canada has tended to focus on large salmonid cage operations in marine coastal waters rather than on inland lakes (Chambers et al. 2001). Freshwater cage culture is now receiving increasing attention as an emerging environmental issue. However, there is limited understanding of the environmental impacts of cage aquaculture, as long-term water-quality data are often lacking.

The depletion of oxygen in the bottom waters of lakes is of particular concern in cage operations (Beveridge 1984). Increased sedimentation of fish waste materials, as well as

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the eventual decomposition of the elevated levels of algae produced, may deplete oxygen in hypolimnetic waters. These anoxic and hypoxic conditions can have severe repercussions for oxygen-dependent organisms, as well as alter processes at the sediment–water interface. For example, deep-water oxygen availability may affect the diversity and abundance of many types of biota, and under anoxic conditions, the release of nutrients (e.g., orthophosphate) can be enhanced, thereby prolonging the effects of eutrophication (i.e., internal loading) (Nürnberg 1995). Enhanced oxygen depletion due to cage farming may be especially problematic in regions within Lake Huron that have been designated "cold water fishery areas", based on Provincial Water Quality Objectives of ≥6 mg·L^{-1} dissolved oxygen (DO) (Ontario Ministry of the Environment (OMOE) 1994).

Although it is suspected that fish farms are responsible for poor water-quality conditions in some lakes (e.g., algal blooms, low hypolimnetic DO conditions), a lack of historical water-quality data is a major obstacle in determining the actual impacts of the cage farms in question. This is particularly the case in the LaCloche Channel (North Channel of Lake Huron), where deteriorating water-quality conditions were linked to cage-aquaculture activities from 1989 to 1998 (Gale 1999*a*). With only limited pre-impact data available, perceived and actual impacts from aquaculture activities in the Channel were questionable. Nevertheless, the aquaculture operation was eventually decommissioned. In the absence of monitoring data, paleolimnological techniques may provide powerful methods for inferring historical water-quality conditions to assess potential environmental impacts in aquaculture areas such as the LaCloche Channel. This information can help to answer important management questions by addressing whether the nutrient-rich status of an aquaculture lake is a recent phenomenon, resulting from intensive fish farming, or a natural condition.

Chironomids (Diptera: Chironomidae) and diatoms (class Bacillariophyceae) are two commonly used paleoindicators that can provide a continuous record of water-quality changes. For example, fossil chironomids are reliable indicators of past oxygen levels (e.g., Quinlan and Smol 2001*a*), whereas diatoms are excellent indicators of past surface-water nutrient levels (e.g., Hall and Smol 1999). In this paleolimnological study we used analyses of fossil chironomid and diatom assemblages archived in the sediments of the LaCloche Channel to track changes in deep-water hypolimnetic anoxia and surface-water nutrient levels, respectively, resulting from aquaculture activities. These data will be used to assess the degree of eutrification and recovery from cage aquaculture in the LaCloche Channel.

Materials and methods

Study area

The LaCloche Channel is located within the North Channel of Lake Huron, Ontario (Fig. 1). The northern shore is bounded by the LaCloche Mountain Range, which is composed primarily of quartzite. Along the south shore, Manitoulin Island borders the Channel and is underlain by dolomitic limestone (Chapman and Putnam 1984). The Eastern Hardwood Forest of North America surrounds the North Channel and is characterized by mixed coniferous and deciduous trees; most of this is second growth because of logging activities during European settlement in the mid-1800s (Sly and Munawar 1988). Historically, this area has been used for a variety of human activities in addition to logging and lumbering, including fur trading, fishing, and mining. Currently, there is little development in the Channel's catchment, with only one cottage and one small fishing lodge.

The LaCloche Channel is characterized by several deep basins (maximum depth 41 m) and a relatively low flushing rate (2.3 times·year^{-1}) (Gale 1999*a*, 1999*b*). This area is managed by the OMOE as a cold-water fishery, which requires minimum DO levels of 6 mg·L^{-1} (OMOE 1994). Historical monitoring data from August 1985 in the forebay of this Channel indicate relatively good oxygen conditions, with hypolimnetic DO levels of 5 mg·L^{-1} and low nutrient levels of <5 µg·L^{-1} total phosphorus (TP) (Gale 1999*b*).

Aquaculture history

Cage farming of rainbow trout first began in the forebay of the LaCloche Channel in 1985 by the Ontario Ministry of Natural Resources and continued until 1992 (Fig. 1). In 1989, commercial fish farming activities began at a site (45°59′52.104″N, 81°45′43.175″W) near the maximum depth (41 m) of the Channel (Fig. 1). Operations began in 1989 with 8 cages and expanded a year later with the addition of a further 10 cages.

Water-quality problems in the Channel were first noted when there was a fish-kill event in 1994. Subsequently, public complaints regarding algal growth in the Channel prompted water-quality testing by the OMOE in September 1997 (Gale 1999*b*). These tests revealed oxygen levels of 5–9 mg·L^{-1} in surface waters (0–12 m) and anoxic conditions at depths greater than 13 m (encompassing the entire hypolimnetic volume over a 250-ha area). TP levels were also elevated and ranged from 16 to 26 µg·L^{-1} for eplimnetic samples and from 18 to 98 µg·L^{-1} for deep-water samples (1 m above bottom) (Gale 1999*b*). The highest eplimnetic TP levels were recorded in October, averaging 40 µg·L^{-1}. At the time of sampling in September, a major algal bloom was visible, and Secchi disc readings were reduced (<4 m). Estimated 1997 loadings from the farm indicated that 1.2 t of phosphorus, 7 t of nitrogen, and 38 t of solid waste were released into the area (Gale 1999*b*). Because of these poor water-quality conditions, the OMOE chose not to renew the land-use permit for the aquaculture company, and by 1 May 1998 all fish cages were removed from the site. Following cage removal, anoxic conditions were still reported in July 1998 (at depths >12 m) and September 1999 (at depths >15 m) (Boyd et al. 2000); however, reductions in nutrient concentrations were found, with autumn 1998 TP levels of 12 µg·L^{-1} (Gale 1999*a*).

Controversy still exists as to whether the fish farm was directly responsible for these poor water-quality conditions, as long-term water-quality data are required to accurately assess impacts. In this case, however, the aquaculture operation was closed, based on a comparison with monitoring data from a one-time sampling event in 1985.

Field and laboratory methods

In late August 1999, a 26 cm long sediment core was obtained from the deep-water region of the LaCloche Channel (38 m depth) at the site where fish cages were located

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(Fig. 1). The core was collected using a Glew (1989) gravity corer (inner diameter 6.6 cm) and sectioned at the lakeshore immediately after collection using a Glew (1988) extruder. The upper sediments (0–10 cm) were extruded at 0.5-cm intervals, whereas deeper sediments (10 cm to the bottom of the core) were sectioned at 1.0-cm intervals. The sectioned sediment samples were placed in individual Whirl-Pak® bags and stored at 4 °C until analyses were undertaken.

To estimate recent dates, sediments were analysed for ^{137}Cs activity in 18 samples taken over the length of the core (Appleby 2001). Wet samples were freeze-dried and subsampled (~0.35 g) into plastic tubes to a height of ~18 mm. These samples were subsequently analysed for ^{137}Cs activity using gamma-counting techniques. Because of insufficient sediment volume, ^{210}Pb activity was not measured.

For chironomid analyses, subsamples of wet sediment (4–22 g) were deflocculated with 5% KOH for ~4 days at room temperature, sieved through a pair of nested Nitex® mesh sieves (200 and 95 µm), and dehydrated with three successive treatments of ethanol (75%, 95%, and 99%). Individual chironomid head capsules were hand-sorted using a Leica® MZ-12 dissecting microscope (8–120× magnification) and mounted on glass slides using Euparal® (refractive index 1.485). If a minimum of 40 head capsules (Quinlan and Smol 2001*b*) were not found, sediments were resampled from freeze-dried material that was used for ^{137}Cs analysis.

Taxonomic identification of chironomids was undertaken using a Leitz Dialux 20 microscope at 125–630× magnification. Head-capsule identifications were based primarily on the structure of the mentum. Specimens with a complete or almost complete mentum were counted as one head capsule, whereas those with approximately half a mentum were counted as a half of a head capsule. Identifications were made according to Walker (1988, 2000) and Wiederholm (1983). The majority of specimens were identified to the generic level, but several taxa had to be combined into higher taxonomic categories because they were indistinguishable. These included *Cricotopus/Orthocladius* and *Corynoneura/Thienemanniella*. Also, a large number of taxa encountered belonged to the tribe Tanytarsina, which is a broad taxonomic group (Walker 1988). Most species from this group are littoral; however, some taxa inhabit the profundal zone, such as *Micropsectra*. *Micropsectra* can be differentiated on the basis of a short apical spur on the antennal pedestal, and a bifid premandible. Premandibles were often missing from our specimens and so we differentiated *Micropsectra* as *Micropsectra* type, primarily based on the presence of a short apical spur.

Diatom slides were prepared for light microscopy following methodology similar to that of Battarbee et al. (2001). A homogenized subsample of ~0.2 g of wet sediment from each core interval analysed was treated with 10% HCl solution to remove carbonate material. Samples were left undisturbed for 24 h to settle and subsequently the supernatant liquid was aspirated. The sediment samples were then washed with deionized water and allowed to settle for 24 h before being aspirated. This rinsing procedure was repeated four times. The organic component of the samples was digested by treatment with an equal mixture by weight of concentrated sulphuric acid (H_2SO_4) and nitric acid (HNO_3), heated in a water bath (~80 °C) for ~5 h, and left to settle for 24 h. Eight deionized water rinses were conducted, as outlined above, until neutral pH was attained. An aliquot of homogenized slurry was then pipetted in a series of sequential deionized-water dilutions onto cover slips. Addition of a small amount of 10% hydrochloric acid (HCl) aided in the dispersion of diatom microfossils on the cover slip. Cover slip samples were evaporated and mounted on glass slides using Naphrax® mounting medium (refractive index 1.74).

Diatom valves were identified and enumerated along parallel transects from the centre of each cover slip, using a Leica DMRB microscope equipped with differential interference contrast optics (numerical aperture 1.30; magnification 1000×). A minimum of 300 valves were counted for each sample. Diatom taxonomy and nomenclature followed that of Krammer and Lange-Bertalot (1986–1991) and Cumming et al. (1995). Two species of *Stephanodiscus* (*S. minutulus* and *S. parvus*) were counted as one taxon because of difficulties in differentiating them under light microscopy.

Numerical analysis

Biostratigraphic zones for both chironomid and diatom assemblages were determined through cluster analysis using constrained incremental sum of squares (CONISS) (Grimm 1991). To compare the major patterns of variation between chironomids and diatoms, the data were summarized by detrended correspondence analysis (DCA) using untransformed data (Birks 1998). In the DCA detrending was by segments, and nonlinear rescaling was implemented (ter Braak and Šmilauer 1998). Finally, the relationship between profundal and littoral chironomid species and samples was evaluated using a principal components analysis (PCA) ordination. The PCA was based on a covariance matrix with relative abundance data using the CANOCO software (ter Braak and Šmilauer 1998).

Results and discussion

Chronology

The ^{137}Cs profile for the LaCloche Channel core was distinct, and displayed the characteristic rise, peak, and decline in activity (Appleby 2001), which reflects historical nuclear testing (Fig. 2). A well-resolved ^{137}Cs peak is observed around 13.5 cm in the core and provides a marker for the 1963 horizon of maximum atmospheric weapons testing prior to a worldwide nuclear test ban treaty. The presence of this distinct peak suggests that cesium mobility through the sediments was not likely, as this would be represented by a more gradual change in cesium level through the upper intervals. For these reasons we are confident that the ^{137}Cs profile is indicating 1963, and that our core covers the period of aquaculture activity, as well as pre-impact conditions. A linear interpolation of sedimentation rates between 1963 and 1999 is not realistic, as sedimentation rates would not likely have remained constant over this time period because of eutrophication. We acknowledge that our geochronology is approximate.

Paleolimnological analyses

Chironomids and diatoms were well preserved and consisted of three distinct communities based on CONISS (Figs. 3, 4). Stratigraphic zones are not, however, identical between indi-

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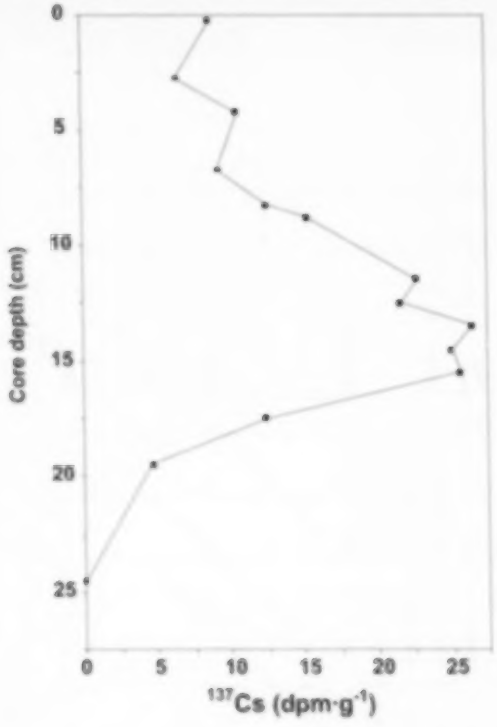
Fig. 2. ^{137}Cs activity in sediments from the LaCloche Channel site.



cators, as diatoms respond positively to nutrient inputs (Hall and Smol 1999), whereas chironomids are mainly benthic and respond to changes in oxygen and food availability resulting from nutrient inputs (Little et al. 2000). Nevertheless, DCA analysis indicates that major shifts in the composition of chironomid and diatom assemblages occurred at similar depths (~9.0 cm for chironomids and ~8.0 cm for diatoms) after 1963 (~13.5 cm) as dated by ^{137}Cs analysis (data are available from the authors). These changes occur in Zone 2 of both chironomid and diatom profiles (Figs. 3 and 4).

A total of 34 chironomid and 78 diatom taxa were identified from the core. There is a clear shift in the composition of the fossil communities from the bottom to the top of the core, with profundal chironomids comprising relatively more of the assemblages in older sediments than in recent sediments. Significant shifts in the diatom community are also evident, most notably in nutrient-sensitive planktonic diatoms, which dominate assemblages throughout the core. Changes in both chironomid and diatom communities are consistent with eutrophication and are discussed in more detail below.

Biostratigraphic Zone 1: pre-impact conditions

Chironomid assemblages deposited during the earliest period of the core indicate well-oxygenated bottom waters, with limited periods of hypoxia (Fig. 3). These conditions are inferred from stable abundances of profundal chironomids characteristic of oxic lakes, such as *Heterotrissocladius*, *Micropsectra* type, and *Sergentia*. *Heterotrissocladius* and *Micropsectra* are well-known indicators of high oxygen levels, whereas *Sergentia* thrives in mesotrophic lakes with moderate oxygen depletion (Quinlan et al. 1998). Sporadically high abundances of *Chironomus*, a taxon highly tolerant of hypoxia (Sæther 1979), indicate that some episodes of low-oxygen conditions may have occurred during this period, possibly as a result of anthropogenic activities in the catchment (e.g., logging). Overall though, the profundal community is dominated by oxic-type taxa, which indicates that hypoxia must have been limited in the Channel prior to the commencement of aquaculture activities.

The composition of the diatom assemblages occurring in Zone 1 indicates oligotrophic to mesotrophic nutrient levels, which is consistent with well-oxygenated conditions in the deeper waters inferred from the chironomids (Fig. 4). For example, high abundances of diatoms characteristic of low to moderate nutrient levels such as *Tabellaria flocculosa* str. IIIP, *Cyclotella pseudostelligera*, *Cyclotella bodanica* v. aff. *lemanica*, and *Cyclotella michiganiana* (Reavie and Smol 2001) are recorded during this period. Moderately rich nutrient conditions during this time are also supported by abundances of *Aulacoseira ambigua*, *Asterionella formosa*, and *Fragilaria crotonensis*, and probably indicate some nutrient enrichment from local human activities in the catchment.

Biostratigraphic Zone 2: inferred aquaculture period

Peak abundances of oxic-type profundal chironomids are observed in the upper portion of Zone 2, including *Micropsectra* type and *Sergentia* (Fig. 3). Shortly thereafter, *Micropsectra* type, a taxon that requires high levels of oxygen (Sæther 1979), declines, followed by the mesotrophic indicator *Sergentia*, indicating progressively lower oxygen availability in the bottom waters. The commencement of fish-farming activities in 1989 may be responsible for lowered oxygen availability in this period. Decreases in oxic-type taxa have been associated with lower oxygen and higher nutrient conditions in other eutrophication studies as well (e.g., Walker et al. 1993; Little et al. 2000; Francis 2001).

Interestingly, declines in these oxic-type indicators are not mirrored by increases in anoxic-type taxa, such as *Chironomus*. For anoxic-type taxa to dominate assemblages, low oxygen and high nutrient concentrations (which affect food availability) are required (Quinlan and Smol 2001*a*). Based on the declines observed in the oxic-type indicators *Micropsectra* type and *Sergentia*, it appears that nutrient loadings from the fish farm were high enough to deplete oxygen levels, but not high enough to sustain profundal populations of anoxic-type taxa (e.g., *Chironomus*), which have high food requirements. In their training set, composed of oligotrophic to mesotrophic lakes, Quinlan and Smol (2001*a*) also found that anoxic-type taxa did not dominate chironomid assemblages in lakes with extremely low end-of-summer oxygen concentrations.

Another notable feature of Zone 2 is the appearance of *Polypedilum* around 9 cm (Fig. 3). This taxon favours organic muds (Sayer et al. 1999) and has been found to dominate extant chironomid assemblages in sediments near cage farms in Lake Letowskie, Poland (Dobrowolski 1987). Although no sedimentation data are available from the LaCloche Channel site, it is likely that loadings were significant to the benthic environment, as an estimated 164 kg of

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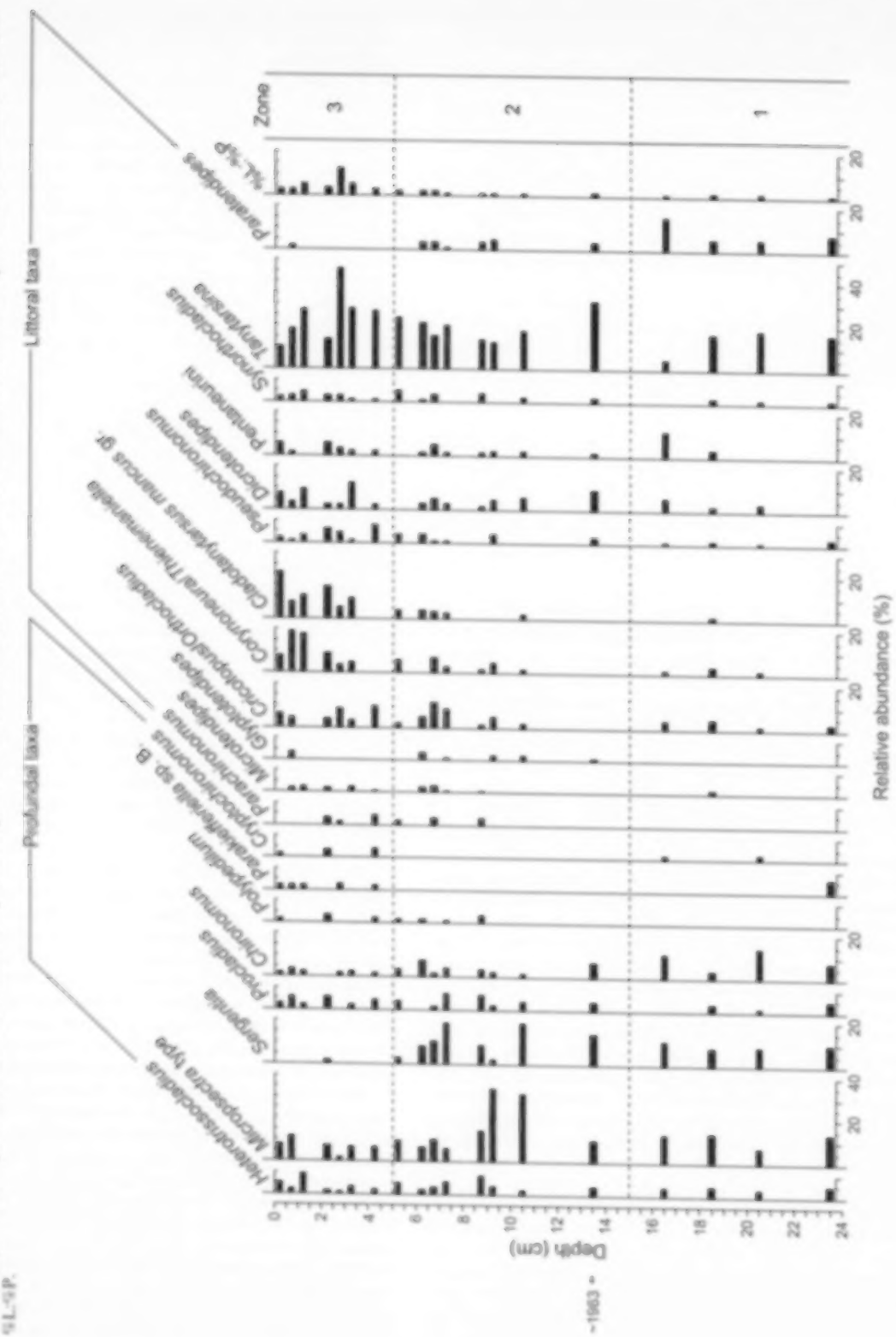

Fig. 3. Relative abundances of the main chironomid taxa in sediments from the LaCloche Channel Profundal and littoral taxa were classified according to the closest available training set to our study area (Quinlan and Smol 2001*a*). Stratigraphically constrained cluster analysis (Grimm 1991) was used to delineate three major zones in the chironomid stratigraphy. ^{137}Cs analysis indicates that the 13.5-cm depth was deposited ~1963. The ratio between the relative abundances of littoral and profundal chironomids is shown as %L:%P.

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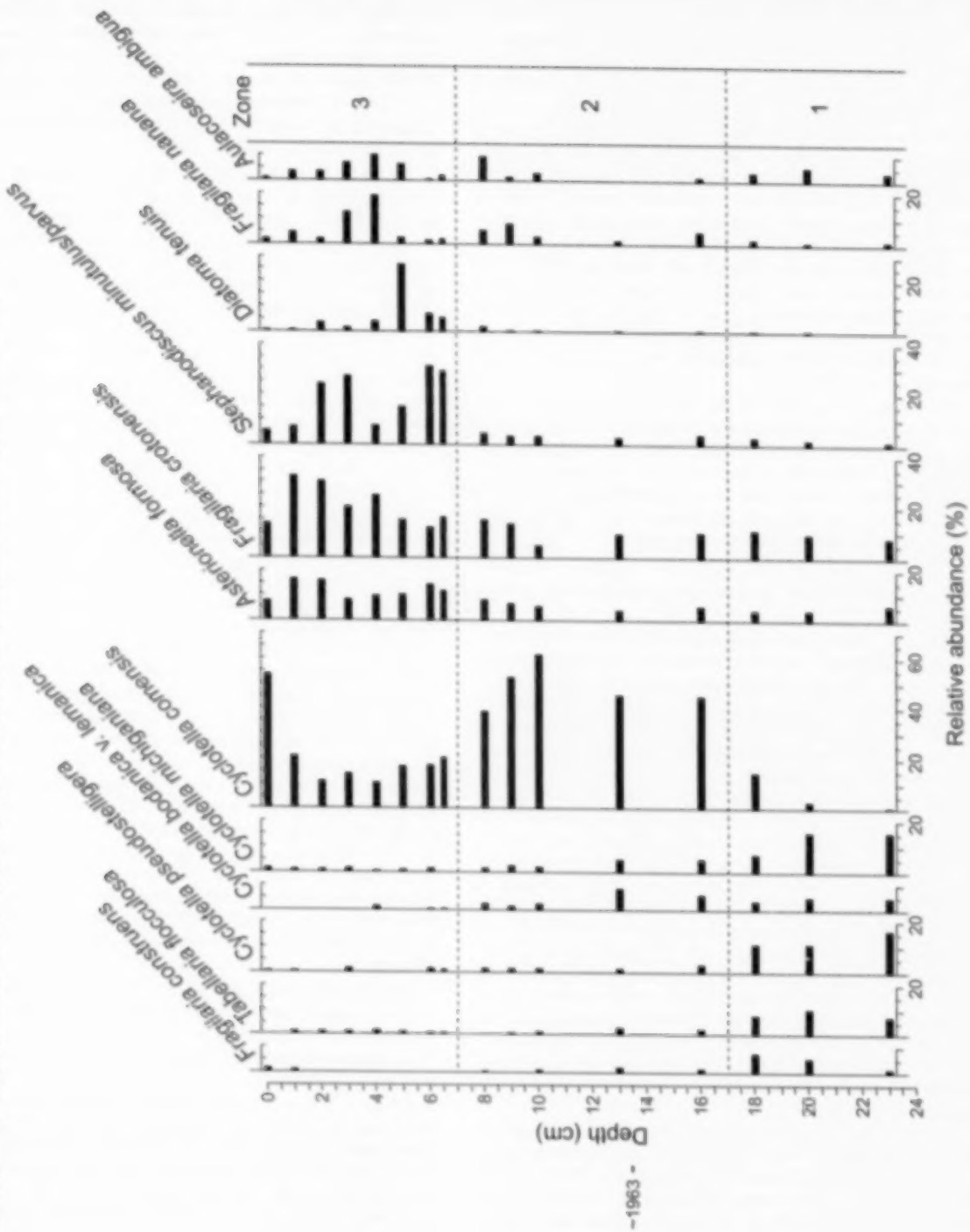

Fig. 4. Relative abundances of the 12 most abundant diatom taxa (>5% in at least two samples) in the core from the LaCloche Channel. ^{137}Cs analysis indicates that the 13.5-cm depth was deposited ~1963. Diatom zones were constructed using stratigraphically constrained cluster analysis (Grimm 1991).

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solid waste can be generated per tonne of fish produced (Cho and Bureau 1998). Thus, the appearance of this taxon may be related to increased loadings from aquaculture activities in the LaCloche Channel.

Changes in the diatom assemblages in Zone 2 provide additional evidence of eutrophication from aquaculture activities (Fig. 4). More productive conditions ~9.0 cm are inferred from increases in several mesotrophic diatom species (e.g., *Fragilaria crotonensis*, *F. nanana*, and *A. ambigua*), coupled with concurrent decreases in relative abundance of the dominant oligotrophic indicator, *Cyclotella comensis* (Reavie and Smol 2001). The increase in *C. comensis* observed earlier in Zone 2 is likely related to increased atmospheric deposition of inorganic nitrogen (NO_3) from industrialization around the Great Lakes system (Pappas and Stoermer 1995). The rise in this taxon, which may be favoured under low-silica and high-nitrate conditions (e.g., during summer blooms), has also been observed in other, typically oligotrophic, parts of the Laurentian Great Lakes (Stoermer and Kreis 1980; Stoermer et al. 1996).

The stratigraphical plot of the DCA sample scores indicates a substantial compositional change in both chironomid and diatom assemblages in Zone 2 (data are available from the authors). Differences in the timing of these changes were minimal between chironomids (9.0 cm) and diatoms (8.0 cm) and, based on our inferred chronology, are approximately coincident with the aquaculture operation.

Biostratigraphic Zone 3: expansion and removal of cage farm

Profundal chironomid assemblages from the most recent sediments in Zone 3 are characterized by the disappearance of *Sergentia*. This provides strong evidence of reduced oxygen availability in deep-water habitats and contrasts sharply with pre-impact assemblages that had stable abundances of this taxon. The disappearance of *Sergentia* has been associated with the development of anoxic conditions in past eutrophication studies (Little et al. 2000; Francis 2001). Other oxic-type profundal taxa are present in similar (e.g., *Heterotrissocladius*) or only slightly reduced (e.g., *Micropsectra* type) abundances compared with background levels. This suggests that low-oxygen conditions were restricted in the Channel, perhaps to the deepest basin, where *Sergentia* thrived. Lower oxygen conditions during this period are also supported by the appearance of *Cryptochironomus* and *Parakiefferiella* sp. B., taxa which, according to Quinlan and Smol (2001*a*), have lower oxygen optima than either *Sergentia* or *Micropsectra* type. Low-oxygen conditions inferred from chironomids during this period are supported by oxygen profiles recorded during the late 1990s, which showed anoxic conditions in the hypolimnion during the late summers (Gale 1999*b*).

Zone 3 is also marked by increased abundances of several littoral taxa. Many of the littoral taxa that dominate recent sediments are associated with macrophytes (e.g., *Corynoneura*/*Thienemanniella*, *Cricotopus*/*Orthocladius*, *Dicrotendipes*; Brodersen et al. 2001) (Fig. 3), suggesting that macrophyte biomass increased in the Channel as a result of nutrient enrichment from the fish farm. This is supported independently by the documentation of some of the macrophytes that these taxa are associated with in the Channel (Morton and Venn 2000). Another littoral taxon that increases markedly in the surface sediments is the *Cladotanytarsus mancus* group. Although this taxon grouping is not associated with macrophytes, previous studies have shown increased abundances during eutrophication (e.g., Quinlan et al. 2002). Our results agree with previous studies that have also shown littoral taxa to dominate assemblages during periods of prolonged anoxia associated with eutrophication (Walker et al. 1993; Little et al. 2000).

The relative increase of the littoral community in the recent sediments is recorded in the proportion of littoral to profundal taxa, which shows that the littoral community makes up a greater proportion of the total assemblage in sediments deposited from about 7 cm to the surface compared with background conditions (Fig. 3). PCA of species and samples from the LaCloche Channel is consistent with these findings, as many of the profundal taxa are positioned near the older, pre-impact sediments, whereas recent sediments are dominated by littoral taxa (Fig. 5). These results suggest that nutrient loading from the fish farm likely resulted in a more eutrophic chironomid community in which littoral taxa benefited, likely through increased habitat availability (e.g., macrophytes), whereas profundal oxic-type taxa were restricted by low hypolimnetic oxygen levels.

Diatoms in most of Zone 3 (e.g., 6.5–1.0 cm) provide strong evidence of continued nutrient enrichment in the Channel (Fig. 4). Greater nutrient levels during this period are inferred from the marked shift from the more oligotrophic indicator *Cyclotella comensis* around 6.5 cm to the eutrophic indicator *Stephanodiscus minutulus/parvus* and to a lesser extent *Asterionella formosa* (Reavie and Smol 2001). *Fragilaria crotonensis*, a taxon that often characterizes ongoing anthropogenic nutrient enrichment (Hall and Smol 1999), increases around 5 cm, providing further support for an interpretation of more productive conditions during this period. An unprecedented peak in relative abundance of *Diatoma tenuis* (~5 cm) is also observed in Zone 3. This taxon is associated with high nutrient environments and can bloom under specific nutrient-enriched conditions in spring (Kreis et al. 1985; Krammer and Lange-Bertalot 1991). The expansion of the fish farm in the 1990s may have been responsible for elevating nutrients in the Channel during this period. Elevated nutrient levels inferred from diatoms are corroborated by water-chemistry data collected during the 1990s (Gale 1999*a*).

Most recent surface sediments (~1 cm to the surface) likely reflect a period of reduced aquaculture operations, as the fish farm was scaled back in 1997 and operations ceased in 1998. These sediments are marked by decreases in nutrient-rich taxa such as *Fragilaria nanana*, *F. crotonensis*, *A. ambigua*, *A. formosa*, and *S. minutulus/parvus*, coupled with a rebound in abundance of the low-nutrient indicator *C. comensis*. These reductions indicate improvements in surface water quality. In contrast, the absence of *Sergentia* from chironomid assemblages in the surface sediments indicates no corresponding improvements in deep-water oxygen levels.

Monitoring data collected in the autumn of 1998, following removal of the fish farm, supports improvements in surface water quality inferred from diatoms, as measured

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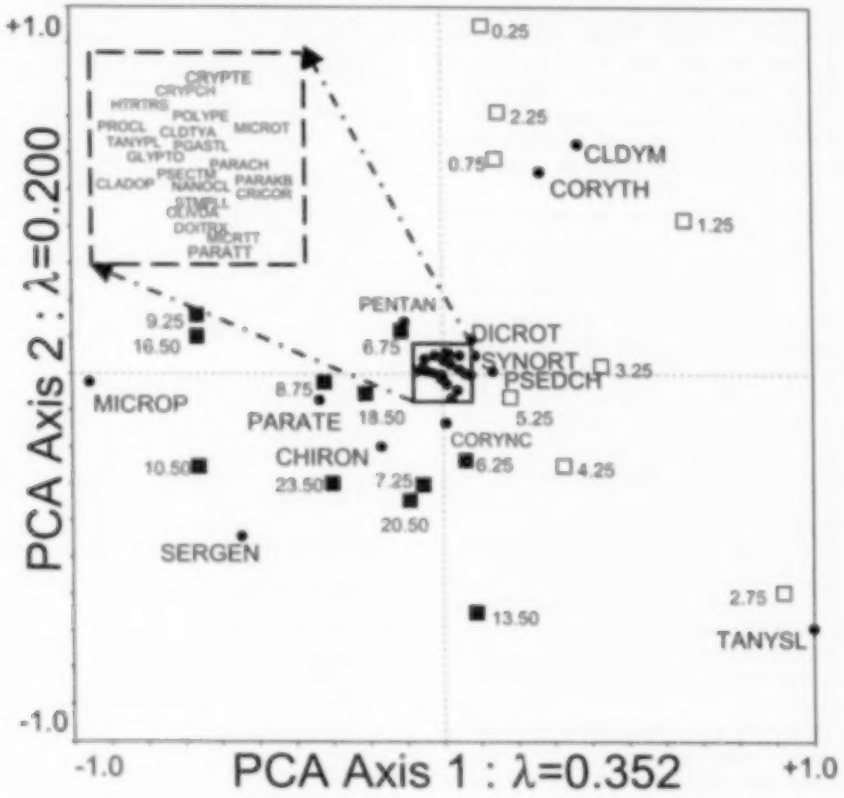
Fig. 5. Principal components analysis (PCA) based on relative abundance data for chironomid taxa greater than 2.0% in at least two intervals and samples in the LaCloche Channel (■, samples from deeper than 5.25 cm; □, intervals ≤5.25 cm). HTRTRS, *Heterotrissocladius*; MICROP, *Micropsectra* type; SERGEN, *Sergentia*; POLYPE, *Polypedilum*; PROCLD, *Procladius*; PARAKB, *Parakiefferiella* sp. B; CHIRON, *Chironomus*; PENTAN, tribe Pentaneurini; CRYPCH, *Cryptochironomus*; CRICOR, *Cricotopus*/*Orthocladius*; PARACH, *Parachironomus*; CORYTH, *Corynoneura*/*Thienemanniella*; MICROT, *Microtendipes*; CLDYM, *Cladotanytarsus mancus* group; TANYSL, tribe Tanytarsina; PARATT, *Paratanytarsus* type; CORYNC, *Corynocera oliveri* type; STMPLLL, *Stempellinella*; PSEDCH, *Pseudochironomus*; DICROT, *Dicrotendipes*; GLYPTO, *Glyptotendipes*; MICRTT, *Microtendipes type*; CRYPTE, *Cryptotendipes*; PGASTL, *Pagastiella*; PARATE, *Paratendipes*; CLADOP, *Cladopelma*; PSECTM, *Psectrocladius* (*Monopsectrocladius*); SYNORT, *Synorthocladius*; NANOCL, Nanocladius; OLIVDA, *Oliveridia*/*Hydrobaenus*; CLDTYA, *Cladotanytarsus* group A; TANYPL, *Tanytarsus pallidicornis* group; DOITRX, *Doithrix*/*Pseudorthocladius*.



average TP levels from several stations in the Channel were significantly lower (12 $\mu g \cdot L^{-1}$) than during operations (40 $\mu g \cdot L^{-1}$). The lack of recovery in hypolimnetic oxygen levels, inferred from chironomids, is also corroborated by DO profiles taken in 1998 and 1999 that indicate the persistence of anoxic conditions (Gale 1999*a*; Boyd et al. 2000).

Sensitivity of the LaCloche Channel to aquaculture activities

Inferences of hypolimnetic anoxia from chironomids and epilemnetic nutrients from diatoms indicate significant changes in bottom-water oxygen conditions and open-water nutrient levels, which are consistent with eutrophication in the LaCloche Channel. The most marked changes in both chironomids and diatoms after ~1963 occurred almost concurrently (i.e., 1 cm apart) and show a clear shift to more productive conditions from background sediments. Furthermore, our inferences of lower oxygen conditions and higher nutrient levels from recent sediments are in agreement with monitoring data. These results suggest significant nutrient loadings to the Channel, most likely because of cage-aquaculture activities.

Our inference that the LaCloche Channel was sensitive to cage-farming activities is supported by site-specific factors that identify the Channel as being more susceptible to eutrophication problems. For example, the deep basins that characterize the Channel could provide isolated depositional zones for fish wastes (Gale 1999*b*). In these areas, oxygen depletion would be enhanced because of restricted mixing between surface and hypolimnetic waters. Leaching of nutrients from solid wastes would be greater in these deeper basins as well, because of the longer time it takes for this organic matter to settle to the bottom (Tlusty et al. 2000). The capacity of the site to assimilate wastes is also thought to be low, owing to restricted exchange rates between the cages and the surrounding water (Hamblin and Gale 2002)

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and the relatively low flushing rate (2.3 times·year^{-1}) (Gale 1999*a*, 1999*b*). These factors would contribute to the Channel being especially sensitive to localized impacts from nutrient loadings.

The maintenance of productive and oxygen-depleted conditions may have been related to the duration and intensification of operations in the Channel. With continued operation and expansion of the fish farm, not only would overall nutrient loadings be greater, but the likelihood of phosphorus release from the sediments under reduced oxygen levels (i.e., internal loading) also increases. Monitoring data gathered in 1997 support this hypothesis, as nutrient levels 1 m from the sediments were extremely elevated (up to 98 μg·L^{-1} TP) (Gale 1999*a*). In past studies, higher nutrient-release rates have also been recorded from sediments at cage sites than at control sites, especially in lakes with longer histories of aquaculture activities (e.g., Kelly 1992, 1993; Temporetti and Pedrozo 2000).

The results of our study imply that recent removal of the cage operation led to improvements in surface water quality but limited, if any, recovery of deep-water oxygen levels by the time of core retrieval in 1999. This indicates that benthic communities may take longer to recover from past aquaculture loadings, compared with planktonic communities. Other eutrophication studies have also described a similar pattern of lake recovery (e.g., Walker et al. 1993; Little et al. 2000). Doughty and McPhail (1995) observed severe impacts on sediments of a vacated cage site in terms of elevated oligochaete abundances, even 3 years after cessation of fish-farming activities, indicating that it may take several years before benthic organisms recover.

The rate of oxygen uptake by sediments may be controlled by past organic loadings (Granéli 1978), so a lag can be expected between declines in sediment deposition rates from fish wastes and sediment uptake of oxygen. In the case of the LaCloche Channel, improvements in oxygen conditions may be realized only after further reductions in TP levels. For example, modelling in the LaCloche Channel (Gale 1999*a*) predicts anoxic conditions in the entire hypolimnion at a TP level of 13 μg·L^{-1}, whereas only 5% of the hypolimnion is expected to be below 6 mg·L^{-1} DO under historic TP levels (5 μg·L^{-1}) (Gale 1999*a*).

In conclusion, knowledge of the environmental impacts of cage aquaculture is critical to the protection and management of aquatic resources, especially considering that the Ontario cage-aquaculture industry is predicted to double production within the next 10 years (Gale 1999*b*). Our paleolimnological data suggest that chironomid and diatom microfossils can effectively track changes in water quality (e.g., hypolimnetic oxygen levels, nutrient levels) associated with cage farming. Moreover, these data may provide information on natural lake conditions that are unavailable from historical data, but necessary for selecting sites, determining actual water-quality impacts from aquaculture activities, and setting realistic mitigation goals (Smol 2002).

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Influence of lake chemistry and fish age on cadmium, copper, and zinc concentrations in various organs of indigenous yellow perch (*Perca flavescens*)[1]

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Abstract: Concentrations of Cd, Cu, and Zn were determined in various organs of juvenile yellow perch (*Perca flavescens*) collected from eight lakes located along a metal concentration gradient. Metal exposure was evaluated on the basis of the free ambient Cd^{2+}, Cu^{2+}, Zn^{2+}, and Ca^{2+} concentrations, as estimated from chemical equilibrium simulations using the ambient water chemistry data. Based on regression analyses, lake water Ca^{2+} and H^+ did not significantly influence the steady-state metal concentrations in various body parts of yellow perch. Cadmium concentrations were significantly higher in the gastrointestinal tract than in the gills, suggesting that uptake of this metal from food is more important than uptake from water. Variations in the contribution of each organ to the total Cd and Cu burdens revealed a possible dysfunction in liver excreting capacities in the fish from the most highly contaminated lakes. Additionally, measurements on yellow perch from 0 to 10 years old ($N = 81$) collected from a single lake suggest that Cd concentrations in some organs increase with fish age, which we interpret to be linked to changes in fish growth rate with age.

Résumé : Les concentrations en Cd^{2+}, Cu^{2+}, Zn^{2+} et Ca^{2+} ont été estimées par simulations chimiques à l'équilibre dans l'eau de huit lacs situés le long d'un gradient de concentrations métalliques. Des perchaudes (*Perca flavescens*) juvéniles y ont aussi été échantillonnées et les concentrations métalliques dans divers organes mesurées. Des analyses de régression ont révélé que les concentrations aqueuses en Ca^{2+} et en H^+ n'influençaient pas significativement les concentrations métalliques dans divers organes des perchaudes. Les concentrations en Cd du tractus gastro-intestinal étaient plus élevées que dans les branchies, suggérant une prise en charge plus importante de ce métal par la nourriture que par l'eau. Les variations de la contribution de chaque organe aux teneurs totales en Cd et en Cu révélèrent une apparente saturation des capacités d'excrétion du foie chez les poissons en provenance des lacs très contaminés par ces métaux. Finalement, des mesures sur des perchaudes âgées de 0 à 10 ans ($N = 81$) échantillonnées dans un unique lac suggèrent que les concentrations en Cd dans certains organes augmentent avec l'âge du poisson, ce que nous interprétons comme un effet du changement du taux de croissance avec l'âge.

Introduction

Metal concentrations in fish have been used extensively as indicators of metal exposure (Ion et al. 1997; Yeardley et al. 1998). In this regard, yellow perch (*Perca flavescens*) offer considerable potential as metal biomonitors, since they are widespread in Canada (from New Brunswick to Alberta) and are found in the United States as far south as Florida (Scott and Crossman 1973). They are also present in a wide variety of habitats, from lakes to small ponds to slow-flowing rivers, in part because they tolerate wide ranges of temperature and pH values as low as 4.8 (Baker and Christensen 1991). Because this fish species is relatively sedentary (Aalto and Newsome 1990), its metal concentrations are generally representative of local conditions. However, the yellow perch's potential as a metal biomonitor is hampered by a lack of data on relationships between metal exposure and metal concentrations in feral individuals.

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Laboratory studies suggest that metal concentrations in a given fish species depend on many factors, such as the exposure concentration and duration (Hansen et al. 2002) as well as metal speciation and the concentrations of competing ions in exposure media (Playle et al. 1993). The preexposure history of metal-exposed fish can also influence their accumulation of metals (Taylor et al. 2000). In the laboratory, fish are usually exposed to metal in water alone, whereas in the field, food can also be an important exposure route. Furthermore, most laboratory metal exposures are at higher concentrations and for shorter durations than would be the case in nature.

These differences between laboratory and field exposure conditions are especially important for fish because most researchers treat these animals as multicompartment systems, that is, they measure metals in various organs (Berninger and Pennanen 1995; Andrès et al. 2000). Metal partitioning among organs is likely to change over time in laboratory fish because they are usually exposed to a sudden change in dissolved metal concentrations: metal concentrations will likely be higher at the site of uptake at the beginning of exposure, but this distribution should change as exposure duration increases and the metal enters the fish's circulatory system. This is less likely to be the case in the field where fish are exposed to metals at more stable concentrations in both food and water. Because there are few published measurements of metals in the various organs of wild perch from lakes of various metal concentrations, we do not know the typical distribution patterns in nature.

The underlying hypothesis of this work was that the distribution of a metal among the organs of wild fish varies along metal exposure gradients and that perturbations in the "normal" distribution occur when a toxic threshold is exceeded. The specific objectives of this study on wild yellow perch were to (*i*) measure the influence of fish age on metal accumulation, (*ii*) relate metal concentrations in fish to those in lake water, and (*iii*) identify the most probable target for metal toxicity among five fish organs. To address the first objective, we measured metal concentrations (Cd, Cu, and Zn) in the various body parts of yellow perch ranging in age from 0 to 10 years that we collected from a single lake. To address the next two objectives, we characterized metal exposure in eight lakes located along a Cd, Cu, and Zn gradient and then measured shifts in relative metal concentrations and burdens among five body parts of juvenile yellow perch as metal exposure increased.

Materials and methods

Study area

The eight study lakes (Table 1) are located in the vicinity of Rouyn-Noranda, a city situated about 600 km northwest of Montréal, Québec, Canada. Metal sources in this region include mineralized rock outcrops, mine tailings, abandoned mines, and the Horne copper smelter (in operation since 1927). Two of the sampled lakes receive localized runoff from nearby mine tailings (Lakes Dufault and Osisko) whereas the others are mainly contaminated by atmospheric emissions. Atmospheric emissions from the smelter are presently largely controlled, but prior to 1985, the smelter was an important source of metals (Cd, Cu, Pb, and Zn) and sul-

Table 1. Location of the lakes sampled in the present study and chemical composition of their epilimnetic water (total dissolved metal concentrations ([*M*]), dissolved organic C ([DOC]), and free metal ion concentrations ($[M^{2+}]$)).

Lake name and location	[Cd] (nmol·L^{-1})	[Cu] (nmol·L^{-1})	[Zn] (nmol·L^{-1})	[DOC] (mg C·L^{-1})	[H$^+$] (nmol·L^{-1})	[Ca^{2+}] (μmol·L^{-1})	[Cd^{2+}] (nmol·L^{-1})	[Cu^{2+}] (nmol·L^{-1})	[Zn^{2+}] (nmol·L^{-1})
Dufault (48°17′N, 79°0′W)	7.72	254	2425	5.5	32	592	3.72	1.5×10^{-1}	1163
Osisko (48°14′N, 79°0′)	2.44	119	466	3.5	631	953	1.41	6.5×10^{-1}	297
Bousquet (48°13′N, 78°35′W)	1.06	56	164	14.7	251	150	0.28	1.7×10^{-2}	54.5
Vaudray (48°05′N, 78°42′W)	0.81	54	109	9.0	112	134	0.18	7.9×10^{-3}	31.5
Héva (48°11′N, 78°19′W)	0.54	35	56	9.4	794	94	0.21	4.5×10^{-2}	26.2
Dasserat (48°13′N, 79°22′W)	0.18	32	57	9.5	32	293	0.03	5.1×10^{-4}	10.4
Ollier (48°11′N, 79°17′W)	0.12	46	23	6.3	13	517	0.03	1.0×10^{-3}	5.6
Opasatica (48°08′N, 79°18′W)	0.11	44	31	7.7	6	337	0.01	2.3×10^{-4}	4.0
Ratio max./min.	70	8	105	4	132	10	372	2826	291

Note: Free Cd^{2+}, Cu^{2+}, Zn^{2+}, and Ca^{2+} concentrations were estimated using the Windermere humic aqueous model (WHAM 6.0.1) from concentrations of total dissolved metal, dissolved Al and Fe, major inorganic cations and anions, DOC, as well as lake water pH.

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phur dioxide to the atmosphere and to lakes downwind from the smelter. Given the physical separation of the sampled lakes, the fish collected from the lakes are considered to be independent observations.

Metal exposure quantification

Water samples were collected in the epilimnion of the eight studied lakes in June 2000 using duplicate in situ diffusion samplers consisting of eight contiguous cells (4 mL) milled into a Plexiglas block and separated from lake water by a polysulfone membrane (0.2-μm nominal pore size; Pall Gelman Sciences, HT-200). Samplers were filled with ultrapure water (Milli Q system water, resistivity ~17 $M\Omega \cdot cm^{-1}$) prior to placement in the lake. The two samplers were suspended 1 m above the bottom and at least 1.5 m under the surface in the epilimnion of each lake. They were retrieved after 3 days and sampled immediately (a sampling period of 3 days had been shown to be sufficient for equilibration of this design of sampler with ambient water; A. Tessier and R. De Vitre, INRS-ETE, 490 de la Couronne, Québec, QC G1K 9A9, Canada, unpublished data). When the diffusion samplers were retrieved, ambient pH and temperature were measured in water collected 0.5 m below the lake surface, above the dialysis samplers, with a portable pH meter (Hannah Instruments, model 9025).

Three replicate samples (3.5 mL) for the determination of trace metal (Cd, Cu, Zn, Al, and Fe) and major cation (Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}) concentrations were removed from each sampler (two samplers per lake for a total of six samples per lake) using a pipette fitted with an acid-washed tip. These samples were injected into prewashed and preacidified (53 μL of 10% HNO_3, Fisher Scientific trace metal grade) high-density polyethylene bottles. Metal and major cation analyses were performed by inductively coupled plasma – atomic emission spectrometry (Varian, Vista AX), except for Cd and Cu, which were measured using a graphite furnace atomic absorption spectrophotometer equipped with a graphite tube atomizer (Perkin-Elmer, Simaa 6000) and an autosampler (Perkin-Elmer, model AS-72). Certified reference water samples (riverine water reference material NIST 1643d, US National Institute of Standards and Technology, Gaithersburg, Maryland) were also analysed for metals during each analytical run; measured trace metal concentrations were consistently within the certified range for each element. Average concentrations were calculated for each sampler resulting in two independent observations for each lake.

Two replicate samples (~1.5 mL) for major anions (SO_4^{2-}, NO_3^{2-}, and Cl^{-}) were also removed from each sampler (two samplers per lake for a total of four replicates per lake) with a pipette fitted with a plastic tip. These samples were injected into polyallomer microcentrifuge tubes prewashed with ultrapure water. Anions were measured by ion chromatography (Dionex, DX300). Two replicate samples (1.5 mL) for inorganic C determination were removed from each sampler using a glass syringe and injected through a septum into preevacuated and prewashed glass tubes; the CO_2 analyses were done using a hot wire detector gas chromatograph (Perkin-Elmer, Sigma 300). Two replicate samples (~4 mL) for organic C determinations were removed from each sampler using a pipette fitted with a tip prewashed with potassium persulfate (1 g per 50 mL) and rinsed with ultrapure water (Elgastat Maxima-HPLC water, total organic C <3 ppb). These samples were injected into amber glass bottles that had been sterilized at 400 °C for 4 h. Organic C was measured using a total organic C analyser (Schimazu, TOC-5000A). Blanks and appropriate standard reference materials for anion measurements and for inorganic and organic C determinations were analysed in accordance with INRS-ETE quality assurance and quality control procedures. Again, average concentrations were then calculated for each sampler resulting in two measurements for each lake.

Metal speciation at equilibrium was calculated for each sampler ($N = 2$ for each lake) with the Windermere humic aqueous model (WHAM 6.0.1) (Centre for Hydrology and Ecology 2001). Input data included major cation concentrations, total dissolved metal concentrations (Cd, Cu, Zn, Fe, and Al), total concentrations of potential inorganic ligands (SO_4, Cl, and CO_3), and organic C. Concentrations of fulvic and humic acids required as input data to WHAM were estimated from our measurements of dissolved organic C: as suggested by Tipping (1994), we assumed that (*i*) humic substances contain 50% C, (*ii*) the ratio of humic to fulvic acids is 1:9, and (*iii*) all dissolved organic C is present as humic substances. The original database of complexation constants provided with WHAM 6.0.1 was compared with recommended values in the US National Institute of Standards and Technology database (Martell et al. 2001) and modified as necessary.

Fish collection and preservation

For the single-lake study, we initially aimed at sampling about 15 fish from each of five size groups (5–10, 10–40, 40–70, 70–100, and >100 g) in Lake Osisko in June 2000 with a seine net or fishing rods. We ended up collecting more than 15 fish in one size group (40–70 g) and less than 15 in the others. The age of each fish was evaluated independently by two observers from fish otoliths as well as from a section of the longest ray of the dorsal fin. There was an agreement between the observers for 96% of the aged fish. When the two observers disagreed, a third observer independently evaluated the age and the age estimated by two of the three observers was assigned. We then selected among all of the sampled fish a maximum of 15 fish per age. Because some age-classes were overrepresented (e.g., the age-1 and age-6 fish classes), we selected the 15 first sampled fish from the initial sample for these two age-classes for subsequent metal analysis. Lake Osisko was chosen because of its intermediate metal concentrations relative to the other lakes of the study region and because it supported a large yellow perch population. After collection, the fish were kept alive until killed with a blow to the head and dissected into five body parts (liver, kidney, gills, gastrointestinal tract, and carcass) plus gastrointestinal contents.

For the multilake study, 15 juvenile fish (7–10 g) were collected by seining from each of eight lakes (Table 1) in June 2000. Fish were kept alive until they were killed with a blow to the head and then dissected into five body parts: liver, kidney, gills, gastrointestinal tract, and carcass. The age of each fish was evaluated independently by two observers from a section of the longest ray of the dorsal fin. There

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was an agreement between the observers for 79% of the aged fish (12% of the disagreement came from a single lake, Lake Bousquet). When the two observers disagreed, a third observer independently evaluated the age and the age estimated by two of the three observers was assigned.

For the single-lake and multilake studies, each body part was kept individually in acid-washed plastic containers at –20 °C. Also, for both studies, gastrointestinal tracts were emptied using a scalpel to push the gastrointestinal contents (food and mucus) out of the tract. This procedure could lead to underestimates in metal content of the gastrointestinal tract if the mucus that was removed contained measurable quantities of metals.

Tissue metal analyses

Metal concentrations and burdens (metal concentration in body part × body part weight) were determined for Cd, Cu, Zn, and Ca in each body part. Frozen tissues were freeze-dried and then weighed. Dried tissues were digested with nitric acid (Fisher Scientific trace metal grade, ~3 mL of acid per gram dry weight of tissue) in an autoclave at 120–125 °C for 3 h. Cooled digestates were then diluted 10:1 with ultrapure water. A certified reference material (lobster hepatopancreas, National Research Council of Canada, NRCC TORT-1) was submitted to the same procedure. Concentrations of Cd, Cu, Zn, and Ca were measured by inductively coupled plasma – atomic emission spectrometry. Blanks indicated negligible contamination ($N = 18$): Cd < 0.33 $\mu g \cdot L^{-1}$, Cu < 0.6 $\mu g \cdot L^{-1}$, Zn < 1.5 $\mu g \cdot L^{-1}$, and Ca = 0.01 $mg \cdot L^{-1}$. The recovery of TORT-1 reference samples ($N = 22$) was within the certified range for Cd (94 ± 3% (mean ± SD)), within 10% of the certified values for Cu (92 ± 3%) and Zn (90 ± 3%) and within 15% for Ca (85 ± 3%).

Calculations and statistics

Condition factors were calculated as $W \cdot L^{-2.96} \times 100$, where W is the fish body weight (grams) and L is the fish fork length (centimetres). The value of the exponent (2.96 ± 0.07 (mean ± SE)) was estimated from the nonlinear regression $W = aL^b$ ($P < 0.001$) using the data from fish collected for the single-lake study. Hepatosomatic indices were calculated as the following ratio: liver dry weight (milligrams)/total body wet weight (grams).

Because the condition of homogeneity of variance was not respected for the raw data (Levene's test for homogeneity of variance, df = 7, $P < 0.001$), fish age differences among lakes (multilake study) were compared using a nonparametric test (Kruskal–Wallis), and a Scheffé test on ranks was used to discriminate among lakes. Similarly, differences in hepatic Cu concentrations among fish from various lakes (multilake study) were tested using a nonparametric test (Kruskal–Wallis). A Tukey honestly significant difference (HSD) test was then performed on ranks to identify those lakes that were different.

To verify the influence of age on metal concentrations in the single-lake study and to investigate the influence of metal exposure on metal concentrations or burdens and on fish condition in the multilake study, we initially examined relationships between variables in bivariate scatterplots. When bivariate plots indicated a possible linear relationship, a simple regression model was tested using the Statistica computer program (StatSoft Inc. 1999). When bivariate plots appeared nonlinear, nonlinear regression models with least-squares fitting were tested using the Sigmaplot computer program (SPSS Inc. 2000); the explained variances were compared with those obtained from a simple regression model. For each of the significant relationships presented, we verified if the residuals were normally distributed and if some outlier values biased the regression coefficients. Lastly, because of the relatively large number of regression analyses done, the Bonferroni procedure was used to adjust the significance level for the individual regressions. The proportionality between Zn^{2+} and Cd^{2+} concentrations in the multilake study was tested using simple linear correlation (Pearson r) and no outliers were identified when the scatterplot of the correlation was examined.

To identify differences among hepatosomatic indices of yellow perch from various lakes (multilake study), a one-way analysis of variance (ANOVA) was used (df = 7) followed by a Tukey HSD post hoc test. The normality of the distribution and the homogeneity of the variances of the dependent variable within groups were verified.

Competition modelling

The free-ion activity model (Campbell 1995) and its more recent derivative, the biotic ligand model (Di Toro et al. 2001), both assume that metal bioaccumulation proceeds via facilitated cation transport across an external membrane, i.e., that the primary interaction of a metal with a living organism involves the binding of the metal to a metal transport site embedded in an epithelial membrane. If this metal transport site is located at an epithelial surface, e.g., the apical or basolateral gill cell membranes, then other aqueous cations could in principle compete with the metal of interest for binding at the transport site (Pagenkopf 1983). Using our field data, we tested for the effects of Ca^{2+}, H^+, and metals on the accumulation of Cd, Cu, and Zn in various body parts of indigenous yellow perch. The model tested has been described in detail by Croteau et al. (1998) and by Pagenkopf (1983).

According to this model, reaction of negatively charged uptake sites ($\equiv S^{n-}$) with metals (M^{z+}) and protons (H^+) can be described by the following equilibrium reactions:

$$(1) \qquad M^{z+} + \equiv S^{n-} \xleftrightarrow{K_M} \equiv SM^{-n+z}$$

$$K_M = [\equiv SM^{-n+z}]/[M^{z+}][\equiv S^{n-}]$$

$$(2) \qquad \equiv SH^{-n+1} \xleftrightarrow{K_a} \equiv S^{n-} + H^+$$

$$K_a = [\equiv S^{n-}][H^+]/[\equiv SH^{-n+1}]$$

where $[\equiv S^{n-}]$ is the concentration of free uptake sites and $[\equiv SM^{-n+z}]$ and $[\equiv SH^{-n+1}]$ are concentrations of uptake sites occupied by metals and protons, respectively. Concentrations of the accumulated metal M_1, $[M_1]_{organism}$, can be described by the following expression:

$$(3) \qquad [M_1]_{organism} = F \frac{[M_1^{z+}]}{K_a + [H^+] + K_a K_{M_2}[M_2^{z+}]}$$

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where F is a proportionality constant, K_{M_2} is the apparent complexation constant for the reaction of a second metal (M_2^{z+}) with the uptake sites, and K_a is the apparent acid dissociation constant for the protonated uptake sites.

Cationic competitive interactions were quantified by performing least-squares optimization using the Sigmaplot computer program (SPSS Inc. 2000). Each cation was tested individually.

Results

Exposure gradient

Metal concentrations in lake water varied markedly among lakes (Table 1). Metal gradients, defined as the ratios of metal concentrations in the most and least contaminated lakes, decreased in the order $[Zn]_d$ (~100) > $[Cd]_d$ (70) >> $[Cu]_d$ (8) for total dissolved metals and $[Cu^{2+}]$ (~2800) >> $[Cd^{2+}]$ (~370) = $[Zn^{2+}]$ (~290) for free metal ions. The pronounced gradient for free Cu^{2+} stems from the extremely low estimates of free $[Cu^{2+}]$ in the reference lakes (Dasserat, Ollier, and Opasatica in Table 1). Metal concentrations in Lakes Dufault and Osisko were much higher than those in the other lakes, likely because they are the only two lakes to receive runoff from mine tailings. H^+ concentrations also showed marked interlake variability (ratio ~130) whereas Ca^{2+} (ratio of 10×) and dissolved organic C concentrations (ratio of 4×) were more constant.

Organ distributions of metals and age effects

Single-lake study (Lake Osisko)

The highest Cd concentrations for perch of all ages were measured in the kidney followed by the liver, gastrointestinal tract, gills, and carcass; the same sequence was observed for Zn concentrations, although the difference between the kidney and the other organs was much more marked than for Cd (Fig. 1). In contrast, Cu concentrations were highest in the liver and declined in the order liver >> kidney > gastrointestinal tract > carcass > gills.

Metal concentrations in some organs showed modest age dependence (Table 2). This age effect was most evident for Cd, the concentration of which increased in two organs (kidney and liver) with increasing age (Fig. 1). In contrast, gill Cd concentrations declined with fish age (Fig. 1; Table 2). Metal concentrations in fish gastrointestinal contents were unrelated to fish age ($P > 0.05$) (Fig. 2*a*), but Cd in the gastrointestinal tract was positively related to Cd in the gastrointestinal contents ($r^2 = 0.12$, $P = 0.004$) (Fig. 2*b*); this relationship is still significant ($P = 0.01$) when the point at the far right hand-side of the graph is removed. The same relationships were also positive and significant for Cu ($r^2 = 0.18$, $P = 0.004$) and Zn ($r^2 = 0.15$, $P = 0.002$).

Multilake study

Although fish from the same size-class were sampled (7–10 g) in each lake, their ages differed slightly. The average age of the juvenile fish collected for the multilake study was 1 year for fish from Lakes Bousquet, Dasserat, Héva, Ollier, and Osisko and 2 years for those from Lakes Dufault, Opasatica, and Vaudray; however, this age difference was significant only for Lakes Dufault and Vaudray (Kruskal–Wallis, df = 7, $P < 0.001$, followed by a Scheffé test on ranks, df = 7, $P < 0.05$). Linear regressions between fish growth rates (length/age) and metal exposure concentrations were tested and no relationships were found ($P > 0.05$).

Cadmium concentrations

For juvenile fish collected from the eight study lakes, Cd concentrations were consistently highest in the kidney followed by the liver, gastrointestinal tract, gills, and carcass (Fig. 3) (i.e., the same order as for the single-lake study on Lake Osisko). Ratios of the highest to lowest Cd concentrations among lakes were greater in the liver, kidney, and gills (20× each) than in the gastrointestinal tract and carcass (7–8×). Among all studied body parts, the liver was the organ whose Cd concentrations best reflected lake water concentrations followed by the kidney, gills, and gastrointestinal tract (Fig. 3; Table 3). Cadmium concentrations in the whole body were not related to those in lake water (Fig. 3; Table 3). Taking into consideration Ca^{2+} competition with Cd^{2+} at biological uptake sites (see Materials and methods) consistently increased the percentage of the variance explained (r^2 in Table 3) for liver, but this difference was not significant ($P > 0.05$, test of difference between two Pearson linear correlation coefficients). Relationships between waterborne free Cd^{2+} and Cd concentrations in the gills and gastrointestinal tract were best explained by hyperbolic relationships ($y = y_0 + (ax)(b + x)^{-1}$; $r^2 = 0.85$ and 0.90, respectively, $P < 0.01$). However, taking into consideration Ca^{2+}–Cd^{2+} competition increased the linearity of these relationships (Fig. 3; Table 3). Neither H^+ nor Cu^{2+} had any competitive effect on Cd accumulation in liver, kidney, gills, or gastrointestinal tract. Competition by Zn^{2+} could not be tested because of a significant positive correlation between this cation and Cd^{2+} ($r^2 = 0.99$, $P < 0.001$).

Copper and Zn concentrations

Copper concentrations were highest in the liver followed by the kidney, gastrointestinal tract, gills, and carcass (Fig. 4*a*). Two organs showed a relationship between exposure to Cu, evaluated as free $[Cu^{2+}]$, and Cu accumulation: the liver ($r^2 = 0.96$, $P < 0.0001$) and the gastrointestinal tract ($r^2 = 0.81$, $P < 0.01$). Copper concentrations measured in livers of fish from Lakes Bousquet, Osisko, and Dufault were significantly different from the Cu concentrations in livers of fish from reference Lakes Opasatica, Ollier, and Dasserat (Kruskal–Wallis, $P < 0.001$, followed by Tukey HSD on ranks, $P < 0.05$) (Fig. 4*b*).

Zinc concentrations were 10-fold higher in the kidney (Fig. 4*c*) than in any other body part (Fig. 4*d*). Perch from lakes Osisko and Dufault had somewhat higher Zn concentrations in most body parts than did fish from other lakes. Although the ambient $[Zn^{2+}]$ gradient was 300-fold between the most and least contaminated lakes (Table 1), ratios in bioaccumulated Zn were only 1.4-fold for the liver, 2.7-fold for the kidney, and 1.7-fold for the gills. Competition for Zn uptake by Cu^{2+}, Ca^{2+}, and H^+ was tested, but no competitive effect was detected in any body part. Competition by Cd^{2+} could not be tested because of a strong positive interlake correlation between ambient Cd^{2+} and Zn^{2+} (see above).

Metal burdens

Cadmium burdens were highest in the carcass followed by the liver (Fig. 5*a*). The relative contribution of the carcass to

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Fig. 1. Relationships between the age of Lake Osisko yellow perch and the concentrations ([*M*]; micromoles per gram dry weight, μmol·g dw^{-1}) of Cd, Cu, and Zn in various body parts. Only curves for significant relationships ($P < 0.05$) are shown; explained variation (r^2) and statistical significance (P) are presented in Table 2. Each point represents the value for a single fish ($N = 81$).

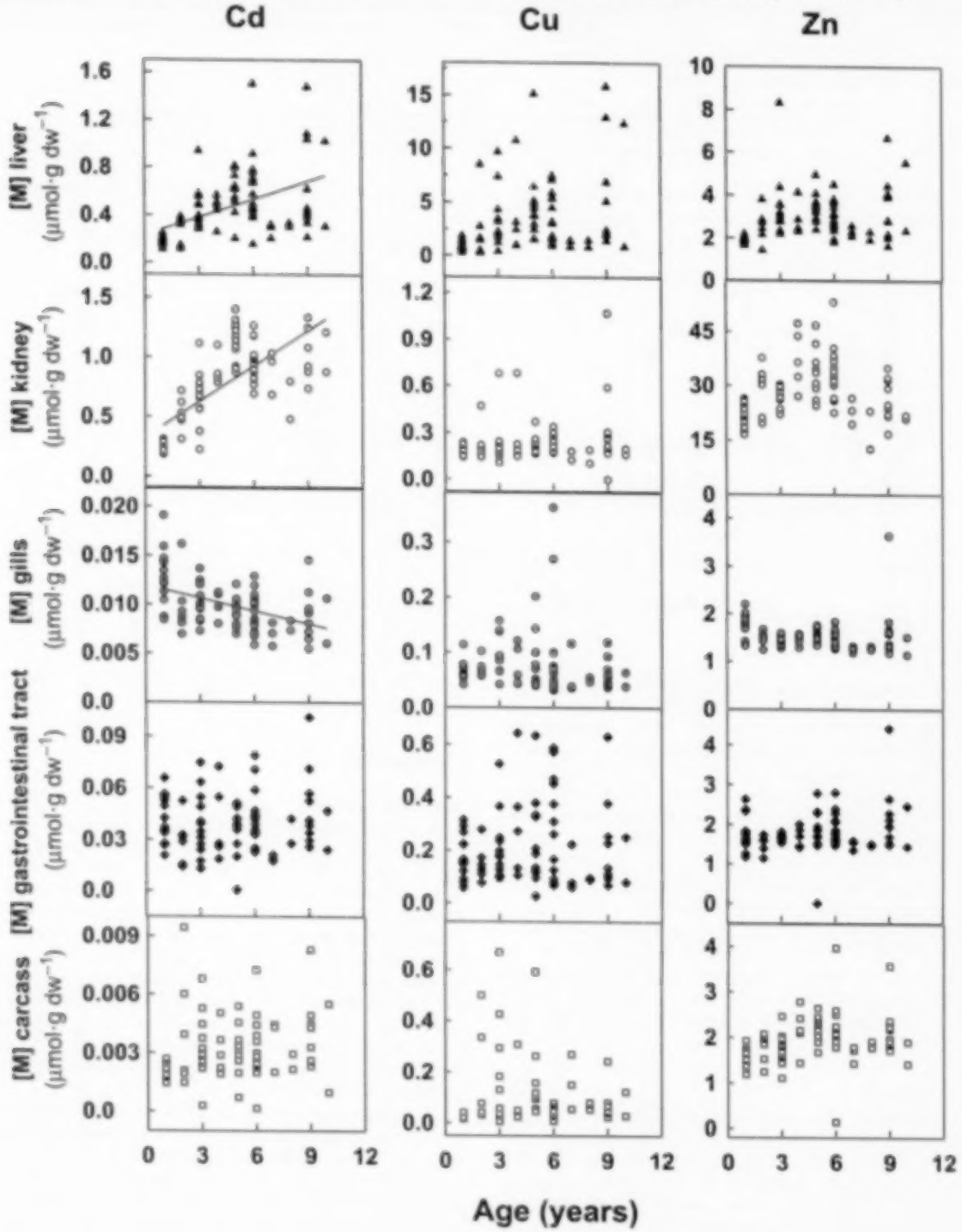

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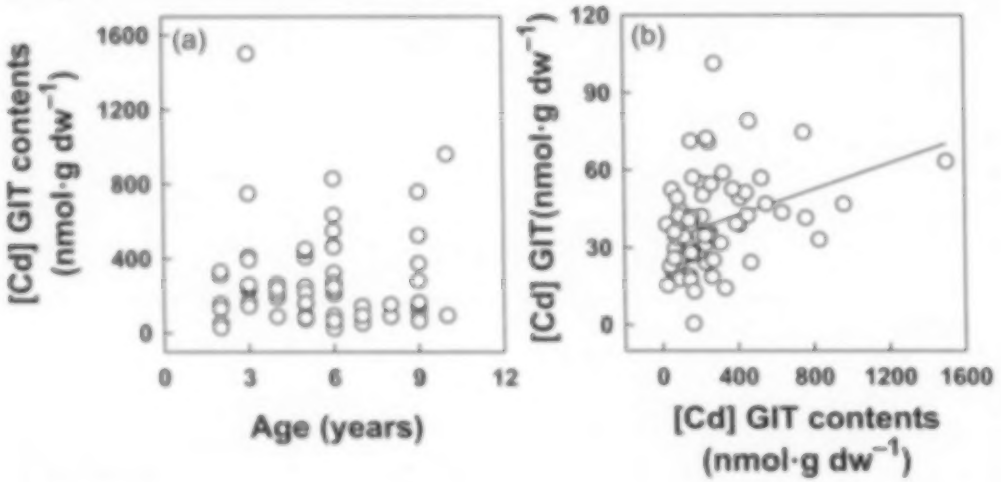
Table 2. Coefficients of determination (r^2) for relationships between fish age and Cd, Cu, and Zn concentrations in various parts of yellow perch from Lake Osisko ($N = 81$).

	Body part				
Relationship	Liver	Kidney	Gills	Gastrointestinal tract	Carcass
[Cd] vs. age	0.23***	0.52***	0.22***	ns	ns
[Cu] vs. age	0.12*	ns	ns	ns	ns
[Zn] vs. age	ns	ns	ns	ns	0.11*

Note: The significance level was adjusted according to the Bonferroni procedure to take into account the number of regressions done (15 regressions). *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; ns, $P > 0.05$.

Fig. 2. Relationships between Cd concentrations (nanomoles per gram dry weight, nmol·g dw^{-1}) in the gastrointestinal tract (GIT) contents and (*a*) fish age or (*b*) Cd concentrations in the GIT ($N = 65$).



the total Cd burden decreased linearly with log[Cd^{2+}] ($r^2 = 0.56$, $P < 0.05$) whereas the liver contribution increased linearly with log[Cd^{2+}] ($r^2 = 0.71$, $P < 0.01$). Similarly, the relative contribution of the carcass to the total Cu burden decreased linearly with [Cu^{2+}] ($r^2 = 0.75$, $P < 0.01$) whereas the liver contribution increased linearly with [Cu^{2+}] ($r^2 = 0.87$, $P < 0.001$) (Fig. 5*b*). In contrast, the relative contributions of each body part to the total Zn burden were not related to Zn^{2+} exposure ($P > 0.05$).

Dry weights of individual body parts were not significantly correlated with log[Cd^{2+}] or [Cu^{2+}] ($P > 0.05$), except for carcass weight, which was significantly positively related to log[Cd^{2+}] ($r = 0.57$, $P < 0.05$). It follows that the observed changes in metal burdens with metal exposure cannot be attributed to changes in the weight of each body part but rather to changes in metal concentrations in the individual organs.

Effects of metals

The condition factor of juvenile yellow perch decreased significantly with increasing liver Cd concentrations (Fig. 6*a*). However, if Lake Dufault is removed, this relationship is no longer significant ($P = 0.2$). The hepatosomatic index of juvenile yellow perch did not decrease significantly with increasing ambient [Cd^{2+}] ($P > 0.05$), but perch from Lake Osisko had significantly lower liver somatic indices than did fish from all lakes except Dufault (one-way ANOVA, $P < 0.0001$, followed by Tukey HSD, $P < 0.05$) (Fig. 6*b*).

Discussion

Single-lake study

A general perception in the current literature is that Cd concentrations do not increase with increasing body size or age within a fish population (reviewed by Sorensen 1991). In contrast, our results show that age is a potentially confounding factor when studying Cd bioaccumulation because Cd concentrations in liver and kidney in yellow perch from Lake Osisko increased with fish age. This observation is not without precedent — other investigators have reported that Cd concentrations in the liver and kidney increased with increasing age in various species of fish from metal-contaminated environments, including Arctic char (*Salvelinus alpinus*) (Köck et al. 1996) and European flounder (*Pleuronectes flesus*) (Rotchell et al. 2001).

To explain age-related increases in Cd concentrations, Köck et al. (1996) proposed a model for long-term Cd accumulation in Arctic char living in alpine Austria in a climate comparable with that found in our study area. This model proposes that a net gain in Cd takes place in summer when ingestion and growth rates are important whereas a net loss of Cd occurs in winter. However, the summer gain in Cd exceeds the loss in winter, resulting in a net annual gain in Cd.

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Fig. 3. Cadmium bioaccumulation in relation to free [Cd^{2+}] (solid line and solid symbols) and to free [Cd^{2+}] normalized for hypothetical competition between Ca^{2+} and Cd^{2+} at biological uptake sites (broken line and open symbols) in the (*a*) liver, (*b*) kidney, (*c*) gills, (*d*) gastrointestinal tract, (*e*) carcass, and (*f*) whole body of indigenous yellow perch. Values of K_{Ca}, explained variation (r^2), and statistical significance (*P*) are presented in Table 3. Each point represents the mean ± SD for 15 fish from each lake. Arrows indicate shifts for (from top to bottom) Lakes Vaudray, Bousquet, and Héva.

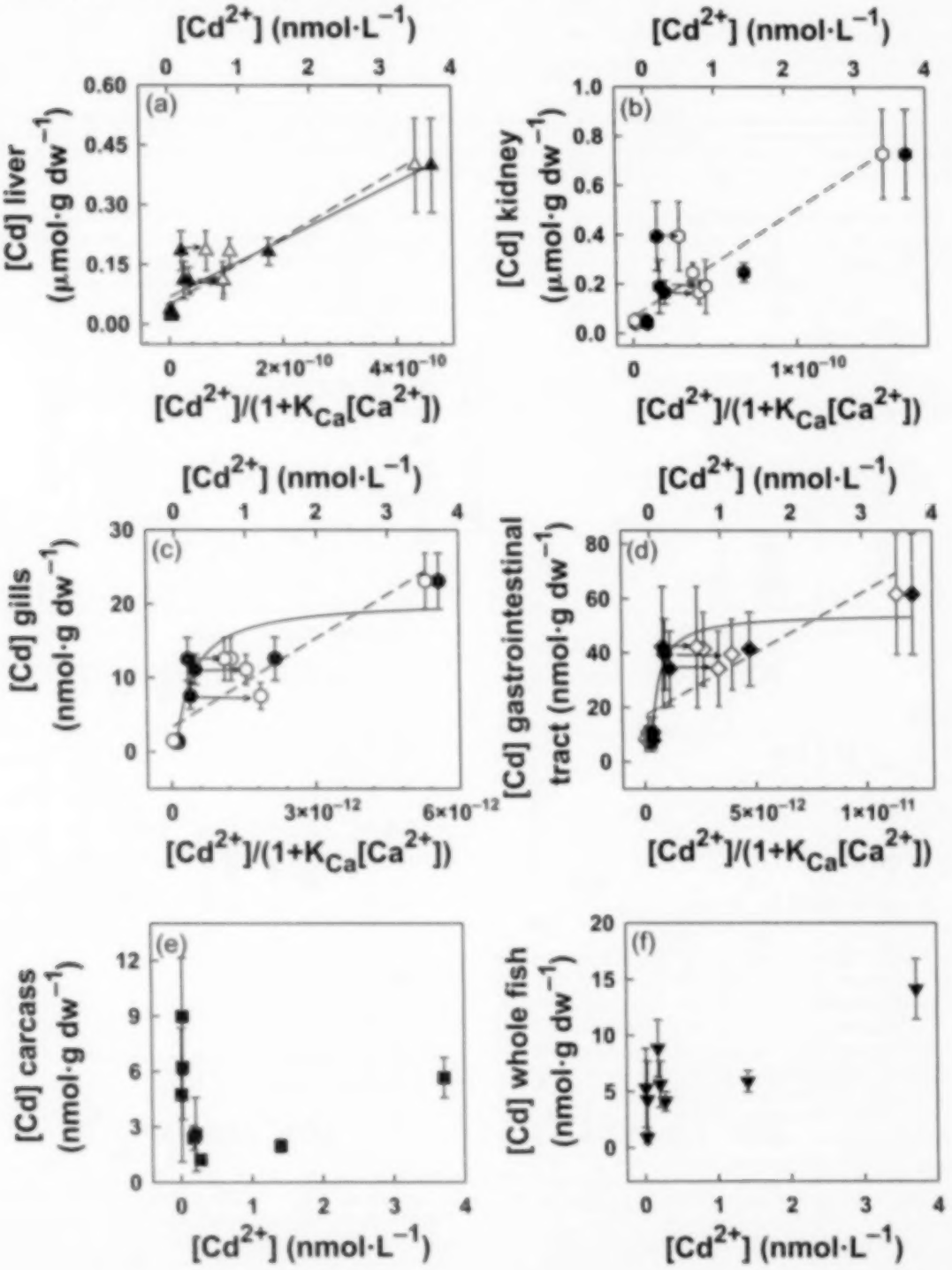

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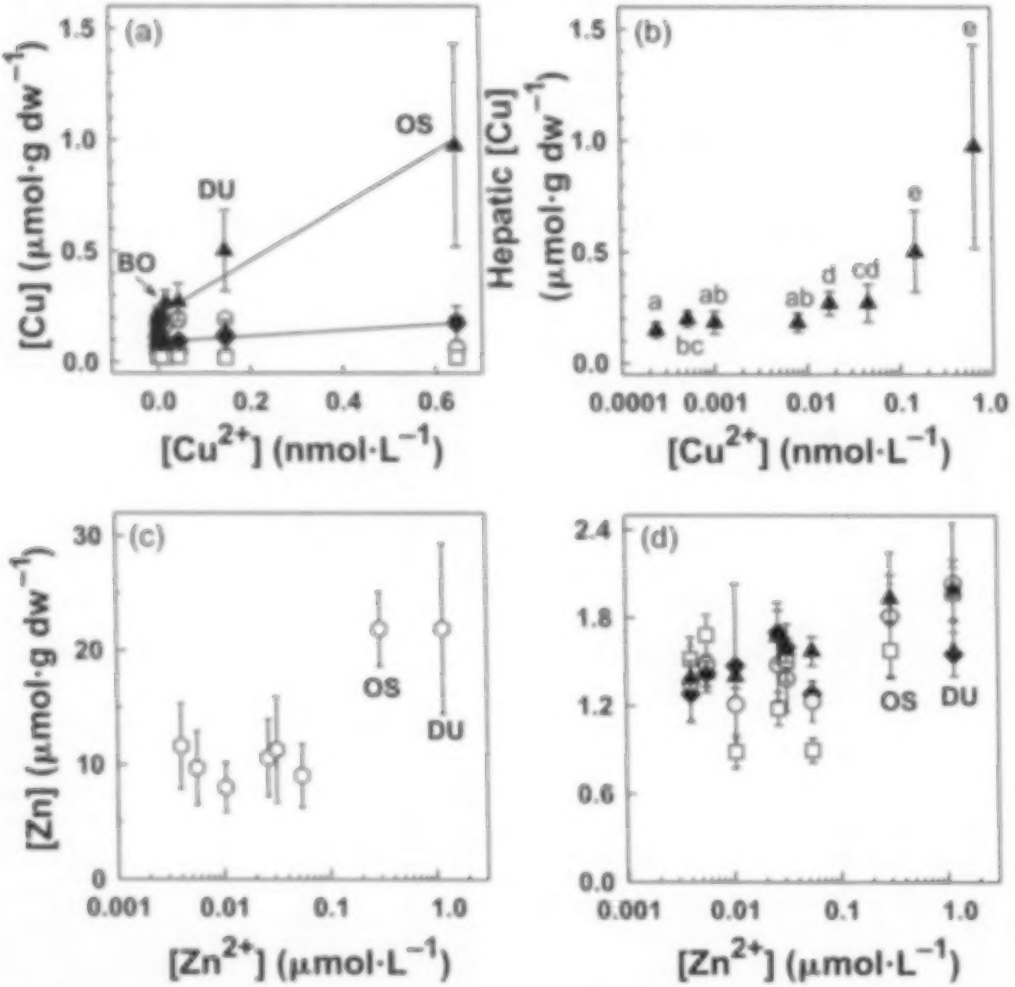
Table 3. Coefficients of determination (r^2) for relationships between Cd accumulation and free [Cd^{2+}] or free [Cd^{2+}] normalized for hypothetical competition with Ca^{2+} at the sites involved in Cd uptake.

	Tissue [Cd]					
Predictor	Whole fish	Liver	Kidney	Gills	Gastrointestinal tract	Carcass
Ambient [Cd^{2+}]	ns	0.85*	ns	ns	ns	ns
Ambient [Cd^{2+}] normalized for Ca^{2+} competition	ns	0.90**	0.87*	0.83*	ns	—
Apparent binding constant (eq. 3)						
K_{Ca}	4×10^4	1×10^4	4×10^4	1×10^6	—	—
SE	9×10^3	2×10^3	5×10^3	1×10^6	—	—

Note: Relationships were examined for whole fish and in various body parts of yellow perch from eight lakes. Estimates of the constant K_{Ca} and associated standard errors are also presented. The significance level was adjusted according to the Bonferroni procedure to take into account the number of regressions done (12 regressions). *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; ns, $P > 0.05$.

Fig. 4. Metal accumulation in various yellow perch parts in relation to free ion concentrations of: (*a* and *b*) Cu and (*c* and *d*) Zn. Each point represents the mean ± SD of 15 fish from each lake. In Fig. 4*b*, different letters beside a lake indicate a significant difference. BO, Bousquet; OS, Osisko; DU, Dufault. Triangles, liver; hexagons, kidney; circles, gills; diamonds, gastrointestinal tract; squares, carcass.



This model agrees with observations of other researchers to the effect that a fast growth rate influences Cd uptake rates and final tissue concentrations (Sorensen 1991).

Dietary preferences and food quality have also been considered as factors to explain age-related increases in Cd concentration, since these variables can affect metal bioaccumulation in wild fish (Sorensen 1991; Andrès et al. 2000). Indeed, yellow perch change their feeding habits as they grow from zooplanktivory to benthivory to piscivory (Sherwood et al. 2002). If metal concentrations in prey items

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Fig. 5. Yellow perch body part contributions to total metal burdens: (*a*) Cd, (*b*) Cu, and (*c*) Zn. Each point represents the mean ± SD for 15 fish from each lake. OS, Osisko; DU, Dufault; OP, Opasatica. Triangles, liver; hexagons, kidney; circles, gills; diamonds, gastrointestinal tract; squares, carcass.

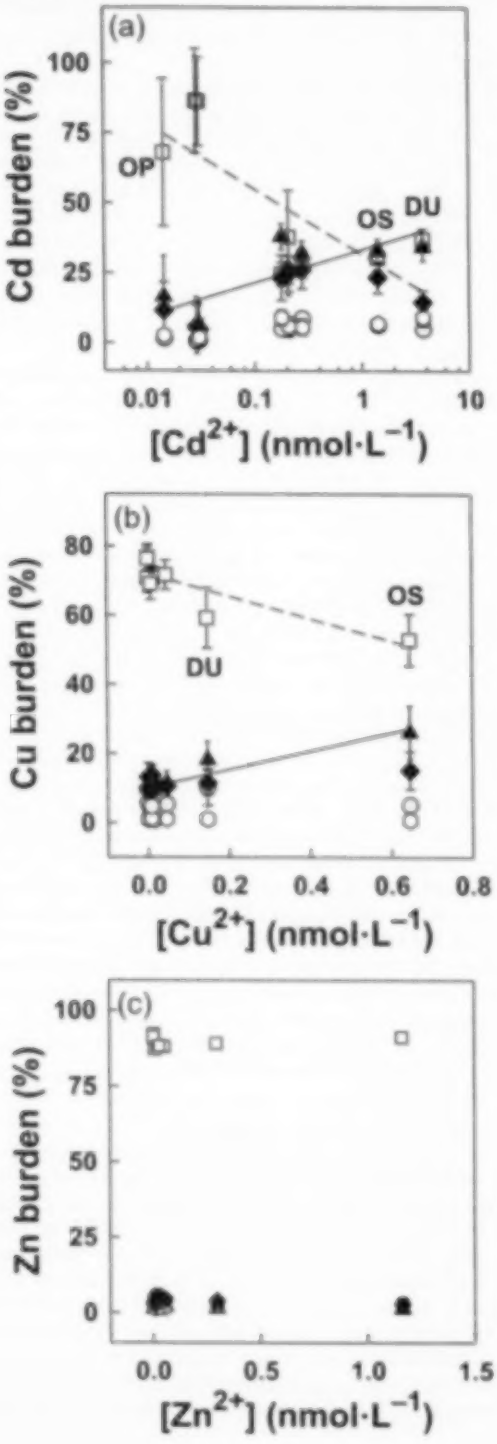
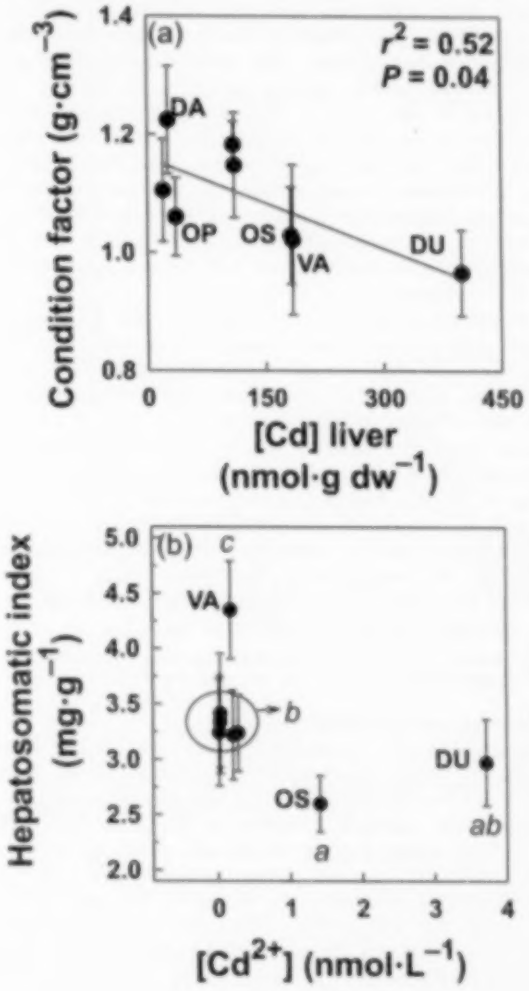


Fig. 6. Relationships between Cd and various biomarkers: (*a*) condition factor in relation to hepatic Cd and (*b*) liver somatic index in relation to $[Cd^{2+}]$ in lake water. Each point represents the mean ± SD for 15 fish from each lake. OS, Osisko; DU, Dufault; OP, Opasatica; DA, Dasserat; VA, Vaudray. In Fig. 6*b*, different letters beside a lake or group of lakes indicate a significant difference.



were to increase in the order planktivorous < benthivorous < piscivorous perch, then the observed increasing tissue Cd concentrations with fish age might be explained by the shift in feeding habits that occurs as yellow perch grow. As a test of this hypothesis, we measured metal concentrations in perch gastrointestinal contents. We assumed that metal concentrations in the gastrointestinal contents are predictors of bioaccumulation, given that gastrointestinal metal concentrations were related to metal concentrations in the gastrointestinal contents. However, metal concentrations in fish gastrointestinal contents proved to be independent of fish age, and thus, we discount the idea that shifts in feeding habits were responsible for the increase in Cd concentrations with fish age.

In contrast with the increase in Cd concentrations noted with fish age in perch liver and kidney, gill Cd concentra-

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tions were lower in older fish. This trend has not been reported previously, likely because most previous researchers did not measure Cd in the gills. The decrease observed in the present study might be explained by a decrease in gill ventilation rates related to a decrease in fish metabolic rates as fish grow. Ventilation volumetric rate (volume of water flowing past the gills per unit time) is reported to be proportional to metabolic rate and both of these parameters decrease as fish grow (Neely 1979). A decrease in ventilation rate leads to a reduction of the speed at which water passes over the gill surface, leading in turn to an increase in the thickness of the layer of unmixed water near the surface. However, according to the biotic ligand model, such changes should not alter the metal uptake rate (the limiting step being the transport across membranes and not the transport from the solution to the surface of the gills: Paquin et al. 2002). A decrease in gill ventilation rate should thus affect accumulated Cd concentrations only if it leads to a decrease in the ventilated surface of the gills.

Relationships between age and Cu or Zn accumulations were weak or nonexistent, a result consistent with the essential nature of these metals. To our knowledge, ours is the first study to measure Cu concentrations in the gastrointestinal tract of indigenous fish, and the dispersion of these data points, for fish of ages >1 (Fig. 1), should be emphasized. This dispersion could reflect the time passed since the last meal of the fish. Indeed, Cu concentrations in the gastrointestinal tract contents (0.5–120 μmol·g dry weight^{-1}) were high relative to Cu concentrations in the gastrointestinal tract itself (0.1–0.6 μmol·g dry weight^{-1}). Such high Cu concentrations in the diet could lead to short-term Cu adsorption on the epithelium of the gastrointestinal tract.

Multilake study

Cadmium concentrations

Relative to other indigenous fish in the order Perciformes (Table 4), yellow perch from Lake Dufault in the Rouyn-Noranda area had the highest Cd concentrations reported in the literature. Laboratory studies on fish other than yellow perch have shown that the distribution of Cd among organs can indicate the route of uptake. In food-exposed fish, Cd concentrations were generally higher in the gut, stomach, and pyloric caeca than in the gills whereas in fish exposed to waterborne metals, Cd concentrations were generally higher in the gills and kidney than in the gastrointestinal tract (Harrison and Klaverkamp 1989; Szebedinszky et al. 2001). If these patterns hold for indigenous yellow perch, then the observation that Cd levels were 3–8× higher in the gastrointestinal tract than in the gills in our study suggests that uptake of this metal from food is more important than that from water. However, higher Cd concentrations in the gut than in the gills do not always reflect contamination by food and could instead reflect a biliary–faecal excretion of Cd; Kraal et al. (1995) demonstrated a higher Cd concentration in the gut than in the gills in a study on common carp (*Cyprinus carpio*) exposed only to waterborne Cd.

The gills have been identified as the site of toxic action of Cd in numerous acute laboratoey water-only exposures (Cusimano et al. 1986; Di Toro et al. 2001); in such cases, gill Cd concentrations have proven to be good predictors of acute Cd toxicity (biotic ligand model approach). However, our results for indigenous yellow perch suggest that the liver and kidney may be important sites for chronic toxicity, since these organs concentrated Cd to the highest levels. Consequently, in seeking relationships between exposure and effects, it seems relevant to model Cd bioaccumulation in all body parts and not only at Cd uptake sites (gills and gastrointestinal tract).

According to our modelling studies, competition between H^+ and Cd^{2+} for biological uptake sites did not have a significant effect on Cd accumulation. Some acute toxicity studies using waterborne exposure have shown that a reduction of pH from 7 to 5 (Cusimano et al. 1986) or from 6 to 5 (Playle et al. 1993) reduced the toxicity of Cd in fish. On the other hand, Schubauer-Berigan et al. (1993) worked between pH values of 8.5 and 6 and observed no effect of pH on Cd toxicity to fathead minnow (*Pimephales promelas*). The H^+ concentrations in our lakes (pH 6.1–8.2) were likely too low to confer any protection against Cd uptake.

Similarly, our calculations revealed only a limited effect of waterborne Ca on Cd accumulation in the liver, kidney, and gills of the yellow perch, although the normalization procedure did improve the linearity of the relationships (note that the points corresponding to Lakes Vaudray, Bousquet, and Héva move to the right). It is somewhat surprising that Ca did not have a more important competitive effect, given its environmental gradient (10-fold) and considering the laboratory studies that have reported an influence of Ca on Cd uptake (Playle et al. 1993) and toxicity (Hollis et al. 2000) in fish at Ca concentrations or gradients that were in the same range as those observed in the present study. One possible explanation for the limited effect of aqueous Ca on Cd accumulation in juvenile yellow perch might be that Cd uptake occurs largely via the diet. Work to date on metal–metal competition modelling in fish has been performed on data from waterborne metal exposures in the laboratory (Playle et al. 1993; Hollis et al. 2000) whereas Cd in indigenous perch may also be taken up from food. Although water hardness is known to affect metal uptake across the gill epithelium (Playle et al. 1993; Hollis et al. 2000), it is less obvious how water hardness would affect Cd uptake from the gastrointestinal tract content in freshwater fish. An in vitro study done by Baskin (1999) demonstrated that Ca had no inhibitory effect on Cd transport across intestinal cells, even though some earlier authors had suggested that Cd may be transported by a Na^+–Ca^{2+} exchanger located in the basolateral membrane of fish enterocytes (Schoenmakers et al. 1992).

Copper and zinc concentrations

With increasing ambient Cu^{2+} concentrations, a steady increase in bioaccumulated Cu concentrations was observed in the liver and gastrointestinal tract of indigenous yellow perch whereas Cu concentrations were regulated in the other body parts. Copper is essential for many functions in the vertebrate body, and complex homeostatic mechanisms are involved in the regulation of its internal levels (Sorensen 1991). Following a review of studies done on yellow perch from 18 lakes located in the Sudbury area, Couture and Rajotte (2003) suggested a value of 50 μg Cu·g dry weight^{-1} (0.8 μmol·g dry weight^{-1}) for basal hepatic Cu concentra-

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Table 4. Metal accumulation by feral fish in the order Perciformes.

Reference	Organ	[Cd] (nmol·g dry weight^{-1})	[Cu] (μmol·g dry weight^{-1})	[Zn] (μmol·g dry weight^{-1})
Perca flavescens				
Our study (Lake Dufault)	Kidney	729	0.19	21.9
	Liver	399	0.50	2.0
	Gills	23	0.12	2.0
	Gastrointestinal tract	62	0.12	1.6
	Carcass	6	0.02	2.0
Couture and Kumar 2003 (Lake Whitson)	Liver	281	1.0	2.8
Eastwood and Couture 2002	Liver		4.04	1.56
Girard et al. 1998 (Iles de la Paix)	Liver	6.4[a]		
Hontela et al. 1995	Liver	6.4[a]	0.03[a]	1.28[a]
Ion et al. 1997	Muscle		0.01[a]	0.0002[a]
Sprenger et al. 1988	Liver	166		1.62
Perca fluviatilis				
Andrès et al. 2000	Kidney	~272[a]		~5.2[a]
	Liver	~176[a]		~1.8[a]
	Gills	~30.8[a]		~2.02[a]
	Intestine	~50.4[a]		~0.86[a]
	Muscle	~0.54[a]		~0.32[a]
Barak and Mason 1990	Liver	8[a]		
	Muscle	1.2[a]		
Berninger and Pennanen 1995	Kidney	32.0		2.3
	Liver	24.5		1.4
	Muscle	0.2		0.6
Carru et al. 1996	Muscle	1.8	0.02	
Hogstrand et al. 1989	Liver		0.02[a]	1.77[a]
Hogstrand et al. 1991	Liver	60.4[a]	0.76[a]	2.14[a]
Olsson and Haux 1986	Liver	56	0.16	1.22
Sjöbeck et al. 1984	Liver	272		

[a]Ratio wet to dry weight used for transformations (empirical ratios from Rouyn-Noranda perch: liver = 4, kidney = 3.4, gills = 4.4, gastrointestinal tract = 2.8, and muscle = 3).

tions in yellow perch. The basal levels in yellow perch from our lakes seem slightly lower: as ambient Cu^{2+} concentration increases, we begin to see appreciable Cu bioaccumulation in perch collected from Lake Bousquet (0.3 μmol Cu·g dry weight^{-1}) and in those collected from Lake Dufault (0.5 μmol Cu·g dry weight^{-1}). Our threshold value is thus slightly lower than that suggested by Couture and Rajotte (2003).

Internal Zn concentrations were regulated in indigenous yellow perch in lakes with ambient Zn^{2+} concentrations up to 45 nmol·L^{-1}; accumulation above basal levels in the kidney, liver, and gills was observed only in fish from lakes with ambient Zn^{2+} concentrations ≥300 nmol·L^{-1}. In a similar study on indigenous fish in the River Lot (France), Andrès et al. (2000) measured no net Zn accumulation above normal Zn tissue levels at a total dissolved Zn exposure concentration of 700 nmol·L^{-1}; uptake above background levels in the kidney and gills was only noted in fish exposed to 1400 nmol dissolved Zn·L^{-1}. Zinc concentrations in the gastrointestinal tract were normally about the same as those in the gills, except for Lake Dufault for which gill Zn concentrations exceeded those in the gastrointestinal tract. This result suggests that in Lake Dufault, the most important accumulation route of Zn may be via lake water, as was found by Bervoets et al. (2001) for indigenous threespine stickleback (*Gasterosteus aculeatus*).

Metal burdens

We examined metal distributions among organs along the exposure gradient to determine if they were altered above a certain metal exposure threshold. For Cd, a shift from carcass to liver as the major organ of accumulation occurred between 0.06 and 0.14 nmol ambient Cd^{2+}·L^{-1}. This shift suggests either that Cd concentrations exceeded the excretory capacity of the liver at this level of exposure or that the liver was storing the excess Cd in detoxified forms such as complexes with metal-binding proteins or as mineral granules. If these detoxification mechanisms were, however, unable to cope with the excess Cd, then it would be free to bind to sensitive sites, such as cytosolic metalloenzymes or mitochondria, with resulting deleterious effects.

A similar trend was observed for Cu. Copper being better regulated than Cd, the change in Cu distribution was small, but it could nevertheless signal the onset of a disturbance in Cu homeostasis in affected lakes (Osisko and Dufault). Because the relative Zn burdens were stable among body parts, the liver must be able to cope with the high concentrations

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of this metal in the most contaminated lakes (Osisko and Dufault).

Effects of metals

The condition factor of native fish reflects their recent growth and energy reserves. The lower condition factors in metal-contaminated fish, especially from Lake Dufault, are likely explained by a direct metabolic impact of the accumulated metals (Levesque et al. 2002). A change in food web structure cannot explain the lower condition factor because fish sampled in our study weighed <10 g, a size-class recognized as planktivorous in yellow perch from these lakes (Sherwood et al. 2002), and zooplankton were abundant in all lakes (J.R. Rasmussen, Department of Biological Sciences, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada, unpublished data). A reduced condition factor was also observed in indigenous yellow perch from a Cu-, Ni-, and Cd-contaminated environment (Eastwood and Couture 2002).

The hepatosomatic index measured in the present study varied between 2.6 and 4.4 but was significantly reduced in only one of the two highly contaminated lakes (Lake Osisko). This index did not respond to metal accumulation in indigenous yellow perch from a Cu-, Ni-, and Cd-contaminated environment (Couture and Rajotte 2003). We conclude that the hepatosomatic index is not a good marker of metal exposure for indigenous yellow perch.

In conclusion, our measurements of metal concentrations in indigenous yellow perch support the use of the liver, kidney, and gills of this species as target organs that respond to Cd exposure. Additionally, the liver and gastrointestinal tract seem to be appropriate as monitors for Cu exposure whereas none of the body parts appears to be appropriate to evaluate exposure to Zn. We also found that Ca concentrations and lake water pH within the ranges measured in our study lakes did not significantly influence metal concentrations in yellow perch liver, but Ca concentrations did influence the prediction of metal concentrations in the kidney and in the gills. From a practical point of view, the liver seems to be the organ best suited for biomonitoring, since its accumulated metal concentrations most closely reflected Cd and Cu exposure. Additionally, we anticipate that liver could be a good organ to monitor the toxic effects of these metals. Indeed, variations in the contribution of each organ to the total Cd and Cu burdens revealed a possible dysfunction in liver excreting capacities in the highly contaminated lakes. Whether or not the excess Cd and Cu that accumulate in the liver lead to toxicity will depend to a large extent on the form in which the metals are stored in the hepatocytes of fish from the highly contaminated lakes: detoxified or toxic forms.

When using adult fish as biomonitors of metal exposure, one should consider the fact that fish age is potentially a confounding factor. We believe that this age dependence of metal accumulation may be linked to fish growth rate. Since growth rate may be highly variable from one fish population to another because of variable environmental factors, yellow perch from other lakes may well not exhibit the same age dependence of metal accumulation as those from Lake Osisko.

We found that higher Cd concentrations were observed in the gastrointestinal tract than in the gills, and this observation supports the idea of a more important uptake of this metal from food than from water. Predominant Cd uptake from the diet could explain the absence of significant competition from Ca^{2+} or H^+ on Cd uptake in all studied organs. If yellow perch are truly taking up the majority of their Cd from food, then the relationship between aqueous and accumulated metals might be further improved by taking into account differences in prey type and prey Cd concentrations among lakes.

Lastly, condition factors were related to Cd accumulation, but much of the variability in this relationship remained unexplained, probably because of the dependence of this factor on multiple environmental parameters. Consequently, on their own, the potential of condition factors as markers of metal effects appears to be limited.

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Site fidelity of slimy sculpin (*Cottus cognatus*): insights from stable carbon and nitrogen analysis

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Abstract: Concerns regarding sentinel species for assessing environmental impacts include residency, abundance, and suitability for measuring responses, if effects are to be attributable to local conditions. Stable isotope analysis was used as a tool to investigate site fidelity of slimy sculpin (*Cottus cognatus*) to establish residency and exposure for the sculpin. We predicted that sculpin collected from sites adjacent to agricultural activity would show higher $\delta^{15}N$ values than those collected from sites in forested areas because of isotopic enrichment by fertilizers in the former. The predominant use of chemical fertilizer applications in the region, however, resulted in no specific enrichment of ^{15}N in sculpin collected in the agricultural region. However, there was an incremental enrichment in the fish muscle tissue of approximately 5‰ in $\delta^{13}C$ values in a downstream direction, irrespective of surrounding land use. As a result, the dual-isotope comparison was successful at demonstrating site-specific isotopic signatures across sites for 30 km of the river system. The site-specific signatures suggest that slimy sculpin are not moving considerable distances among sites and are incorporating their isotopic signatures over a narrow spatial scale. The results support the use of the slimy sculpin as a sentinel species for investigating site-specific environmental impacts.

Résumé : Les préoccupations associées à l'utilisation des espèces sentinelles pour l'évaluation des impacts environnementaux incluent leur résidence dans le milieu, leur abondance et leur aptitude pour la mesure des réactions, si l'on veut attribuer les effets aux conditions locales. Une analyse des isotopes stables nous a servi à évaluer la fidélité au site de chabots visqueux (*Cottus cognatus*) afin de déterminer la résidence et l'exposition de ce poisson. Nous avons prédit que des chabots récoltés dans des sites adjacents à des activités agricoles devraient avoir des valeurs de $\delta^{15}N$ plus élevées que d'autres provenant de sites forestiers, à cause de l'enrichissement en isotopes provoqué par les engrais. Cependant, l'utilisation généralisée d'engrais chimiques dans la région n'a pas causé d'enrichissement spécifique de ^{15}N chez les chabots récoltés dans la zone agricole. Il y a toutefois un enrichissement progressif de $\delta^{13}C$ de l'ordre de 5 ‰ dans le tissu musculaire des poissons vers l'aval, quelle que soit l'utilisation des terres adjacentes. En conséquence, la comparaison à l'aide des deux isotopes réussit à révéler des signatures isotopiques spécifiques pour des sites répartis sur 30 km du système hydrographique. Ces signatures spécifiques au site laissent croire que les chabots visqueux ne se déplacent pas sur de grandes distances d'un site à l'autre et qu'ils obtiennent leurs signatures isotopiques sur une échelle spatiale restreinte. Ces résultats viennent appuyer le choix du chabot visqueux comme espèce sentinelle pour l'évaluation d'impacts environnementaux spécifiques à un site.

[Traduit par la Rédaction]

Introduction

Aquatic environmental effects monitoring programs have generally favoured large-bodied fishes because of ease of collection, tissue size requirements for analysis, value placed on species because of public or commercial importance, and comparability to historical monitoring programs. Some of the limitations of larger-bodied fish species include their potential for movement over large distances and the challenges in determining the stressors associated with changes where there are multiple discharges that occur in relatively close proximity. Recently, there has been increasing attention given to less mobile, small-bodied fishes that may sometimes be more appropriate as monitoring species (Gibbons et al. 1998; Fitzgerald et al. 1999; Tetreault et al. 2003). The Canadian Environmental Effects Monitoring program has seen a progressive increase in the use of smaller forage fish species in the fish surveys (Munkittrick et al. 2002). Many small-bodied fish species have smaller home ranges than traditional monitoring species and so may help overcome some

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of the challenges and problems associated with wide-ranging, larger fish species. Two criteria for choosing an appropriate monitoring species are (*i*) the ability to reflect ambient local conditions and (*ii*) its exposure and residency within a zone of impact (Gibbons 1997; Munkittrick et al. 2000). We were interested in evaluating the suitability of the small-bodied slimy sculpin (*Cottus cognatus*) for use as a monitoring species for studying the non-point source impacts of agriculture on fish populations.

The slimy sculpin lacks a swim bladder and maintains a largely cryptic lifestyle beneath cobble and other instream cover, precluding significant geographic mobility. The male sculpin guards a nest during spawning and rearing of the young (Van Vliet 1964). Mark–recapture studies involving freshwater sculpin species have found that home ranges and movements of recaptured fish were generally <50 m (McCleave 1964; Hill and Grossman 1987; Morgan and Ringler 1992). Recently, we used passive integrated transponder tags to track individual slimy sculpin within a study area of about 1200 m^2 (140-m-long stream section) (Gray 2003). With a recapture rate for tagged sculpin of 37%, we measured 56 movements resulting in a median displacement of 11.3 m over a 10-month period. The major weakness of the mark–recapture study was the relatively low recapture of individual sculpin by electrofishing. Although the study was informative, there was no way to determine whether the tagged fish that were never recaptured were dead, had moved out of the study area, or were still present but were simply not captured.

Conventional approaches to determining animal site fidelity have included measuring a shift in location of use by an animal over time or testing whether there has been a shift in the time spent in different areas (White and Garrot 1990). Stable isotopes offer a unique and potentially less labour-intensive way to look at site fidelity and residency that does not rely on the recapture of individual fish. Assuming an animal resides in a particular area, it will be feeding in that area and thus acquires an isotopic signature from the food sources from that area. The food sources in turn will obtain their isotopic signatures from the local organic matter, which will have certain $^{13}C/^{12}C$ ($\delta^{13}C$) and $^{15}N/^{14}N$ ($\delta^{15}N$) ratios (Hershey and Peterson 1996). Therefore, animals feeding in a particular area will integrate a unique isotope composition as a function of the localized biogeochemical processes (Fry et al. 1999). Harrington et al. (1998) used $\delta^{15}N$ values to distinguish natal streams of Atlantic salmon (*Salmo salar*) in agricultural catchments. They found a positive correlation between the percentage of agricultural land within a catchment and the $\delta^{15}N$ signature of both stream nitrate and fish tissues. Hebert and Wassenaar (2001) also found a strong positive relationship between $\delta^{15}N$ in juvenile mallard feathers and the percentage of land in agricultural use. Owing to intense agricultural cultivation in the lower part of the Little River catchment (northwestern New Brunswick, Canada), we predicted that there would be a similar enrichment of stream nitrate in reaches draining agricultural lands because of fertilizer application and subsequent runoff. Based on the assumption of limited mobility for this fish species, we hypothesized that the enrichment of nitrogen from fertilizer inputs into the stream would be reflected in the $\delta^{15}N$ signature in the sculpin and could be used to discriminate fish from different land-use regions. The alternative hypothesis would be that if sculpin were moving significantly throughout the system, they would have overlapping isotopic signatures reflecting the incorporation of food sources from across a wider spatial and temporal scale. Our main objective was to use stable isotope analysis as a tool to assess mobility of the slimy sculpin and possibly overcome the deficiencies associated with mark–recapture methods.

Methods

Study site

As part of a larger study looking at the health of fish populations in agricultural regions, a sculpin-monitoring study (1999–2001) was designed in the Little River catchment, north of Grand Falls, New Brunswick. The Little River is a 4th-order stream with a catchment area of approximately 340 km^2, which originates in a forested landscape and drains predominantly agricultural lands in its lower reaches (Fig. 1). Sites selected for inclusion in the stable isotope study were classified based on the dominant surrounding land cover that was forested (sites 1–5), a transition area between forestry and agriculture (site 6), and the area where agriculture is the predominant land use (sites 7–10; Fig. 1). Approximately 15% of the total catchment area is under potato cultivation, with all agricultural activities located below site 5.

Fish and sample collections

Sculpin were collected using a backpack electrofishing unit (Smith-Root C-15, Vancouver, Washington, USA). The primary objective at each site was to collect 100 sculpin to assess site-specific population distributions (Gray et al. 2002). All captured fish were measured for length (±1 mm) and weight (±0.01 g) and the 30 largest sculpin were kept for lethal sampling (Gray 2003). The remaining fish were returned to the site of collection after measurements were taken. The collections for stable isotope analysis reported here were made in November 1999 (10 sites), with additional sampling in March and November 2000 and in April 2001 (3–4 sites) to investigate the temporal variability of the stable isotope signatures in the sculpin. The number of sites where fish were sampled was reduced after November 1999, as sites were directed at the study of agricultural impacts (Gray 2003).

Sculpin carcasses were frozen until a sample of epaxial muscle tissue (approximately 40–400 mg) was dissected ventral to the dorsal fin. Tissues samples were air-dried in glass scintillation vials at 50–60 °C for 48 h and then ground to a fine powder using a mortar and pestle. Lipid extraction was not performed, since mean carbon to nitrogen ratios (C/N, a strong indicator of lipid content) for muscle tissues at all sites were within a narrow range (3.3–3.4). McConnaughy and McRoy (1979) considered C/N ratios of 4 as normal and >4 as fatty tissue, with lipid normalization having little influence on non-fatty tissues. Subsamples of 200 µg were analyzed with a continuous-flow isotope-ratio mass spectrometer (Finnigan Mat Delta Plus, Thermo Finnigan, Bremen, Germany) equipped with a ThermoQuest (model NC2500, Thermo Finnigan) elemental analyzer. Isotope ratios in the samples were reported relative to international

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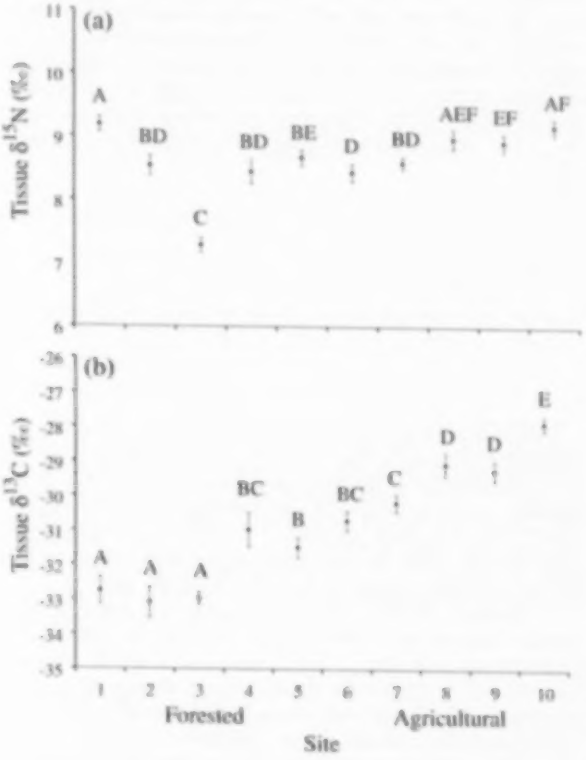
Fig. 1. Schematic map of the Little River catchment (47°03′08.4″N, 67°44′20.8″W; New Brunswick, Canada), indicating sites where slimy sculpin (*Cottus cognatus*) were collected for stable isotope analysis. Sites 1–5 were located within the forested region, site 6 was within a transitional region influenced by both forest and agricultural inputs, and sites 7–10 were located within the agricultural region.

Fig. 2. Mean (±95% confidence interval) $\delta^{15}N$ (*a*) and $\delta^{13}C$ (*b*) isotope values (‰) in slimy sculpin (*Cottus cognatus*) muscle tissues. Site numbers progress downstream from the forested region (1–5), the transition region (6), and into the agricultural region (7–10). Statistical differences between sites are denoted with different letters (Tukey's honestly significant difference test, $p < 0.05$).



reference materials; Pee-Dee Belemnite for $^{13}C/^{12}C$ ($\delta^{13}C$) and atmospheric nitrogen for $^{15}N/^{14}N$ ($\delta^{15}N$). Results are expressed as parts per thousand (‰) deviation from the reference materials.

Evaluation of the repeatability of the machine over time with replicate analyses of the same sample ($n = 35$) resulted in an average $\delta^{13}C$ value of –27.82‰ ± 0.13‰ (standard deviation, SD) and a $\delta^{15}N$ value of 9.04‰ ± 0.16‰ (SD). Precision for internal reference material run concurrently with the samples was ±0.2‰.

Data analysis

Data were assessed for normality by visual examination of normal probability plots, and homogeneity of variance was assessed by visual examination of residual plots. Deviations from normality for isotope data were not strong and were considered negligible when using analysis of covariance (ANCOVA), which is considered moderately robust to small deviations. ANCOVA was used to assess isotopic differences between sites using the logarithm of fish length as a covariate to account for variability due to fish size. Post hoc analysis of differences between sites for ANCOVA was done using Tukey's honestly significant difference test. Statistical analyses were completed using SYSTAT® (SPSS Inc. 1999).

Results

Contrary to our predictions, there was no differentiation of sculpin attributable to enrichment of ^{15}N in the agricultural region (Fig. 2*a*). The three most upstream forested sites (sites 1–3) were the most variable, with mean $\delta^{15}N$ values differing by approximately 2‰. Moving downstream, adjacent sites were similar, with mean $\delta^{15}N$ values within 1‰. Despite such a narrow range, there was a statistical difference among sites (ANCOVA, $F = 59.01$, df = 9, $p < 0.0001$). Sculpin at site 3 had significantly lower $\delta^{15}N$ values than those at any other site along the river, most likely because of groundwater inputs from a tributary immediately upstream of the collection site. There was slight enrichment of ^{15}N in the lowermost agricultural sites (sites 8–10), but these were not significantly different than the uppermost forested site (site 1).

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Fig. 3. Crossplot of mean (±95% confidence interval) $\delta^{15}N$ and $\delta^{13}C$ isotope composition of slimy sculpin (*Cottus cognatus*) muscle tissues. Site numbers progress downstream from the forested region (1–5), the transition region (6), and into the agricultural region (7–10). Site-specific isotopic signatures are more evident and overlap generally occurs only between adjacent sites.

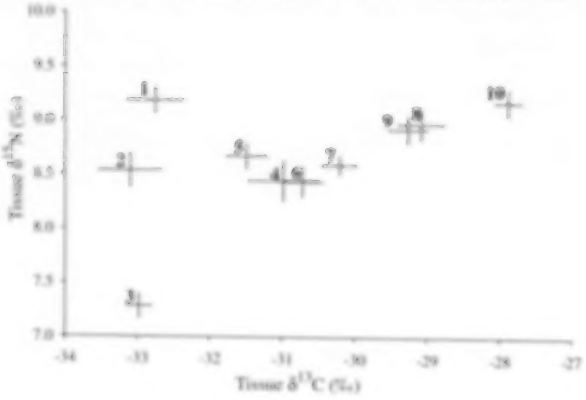
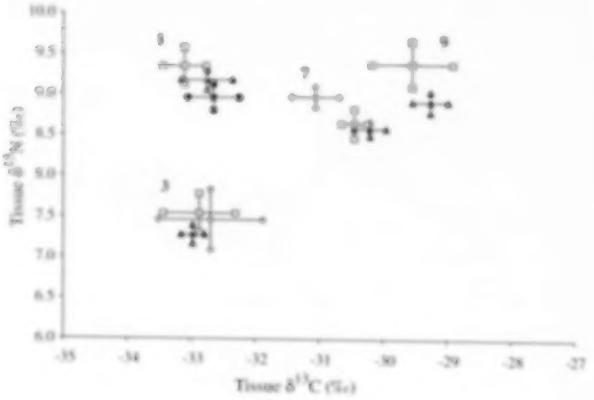


Fig. 4. Temporal variation in mean (±95% confidence interval) $\delta^{15}N$ and $\delta^{13}C$ isotope composition of slimy sculpin (*Cottus cognatus*) muscle tissues collected at particular sites on the Little River. November 1999, solid triangles; March 2000, open diamonds; November 2000, solid circles; and April 2001, open squares.



Differences in $\delta^{13}C$ among sites were more apparent, increasing downstream (Fig. 2*b*). ^{13}C values in sculpin muscle were significantly enriched from approximately –33‰ in the forested region to –28‰ at the lowermost agricultural site (ANCOVA, $F = 84.56$, $df = 9$, $p < 0.0001$). The highest $\delta^{13}C$ value was found at the lowermost agricultural site (site 10), which was significantly higher than all other sites.

A crossplot of $\delta^{15}N$ and $\delta^{13}C$ provides evidence of site-specific isotopic signatures (Fig. 3). With the exception of a small switch with sites 4 and 5 and sites 8 and 9, adjacent sites are more isotopically similar to one another than more geographically distant sites along the river continuum.

Temporal analysis of isotope signatures at selected sites shows that carbon and nitrogen isotopes did not vary significantly within sites (Fig. 4). Over a period of 18 months, average isotope values differed by approximately 0.3‰–0.9‰ for $\delta^{13}C$ and 0.3‰–0.5‰ for $\delta^{15}N$. In general, the spring tissue samples were slightly depleted in ^{13}C and slightly enriched in ^{15}N.

Discussion

The $\delta^{15}N$ of slimy sculpin collected at various sites along the Little River differed significantly, but the difference was not related to any enrichment in stable nitrogen isotopes in the agricultural region as predicted. Sculpin tissues, however, showed a progressive enrichment in ^{13}C along the river gradient from the forested to the agricultural region. Using a dual isotope approach, we showed that site-specific signatures were evident with adjacent sites showing the most similarity, suggesting that sculpin were not moving significantly between sites. The nature of the site specificity of the stable isotope signatures also suggests that the sculpin were reflecting local conditions, likely because of a high degree of residency.

Stable isotopes have been used extensively to investigate food web structure and possible food sources, but have more recently gained attention as a tool for studying movement and behaviour of animals. Hansson et al. (1997) used point-source $\delta^{15}N$ input from a sewage treatment plant to assess movement patterns of fish in the Baltic Sea. They found that more mobile species tended to integrate the characteristics of many areas and thus became more isotopically homogeneous. Kline et al. (1998) used natural, stable, carbon isotopes to indirectly determine migratory behaviour of coregonids based on marine versus freshwater carbon signals. Harvey and Kitchell (2000) investigated movement patterns of many fish species in western Lake Superior using the adjacent cities of Duluth and Superior as a point source of anthropogenically enriched ^{15}N. The slimy sculpin was the only fish species that showed ^{15}N enrichment, with site as a significant factor for its isotopic signature, indicating its sedentary nature. Conversely, rainbow smelt (*Osmerus mordax*) showed no differences in $\delta^{15}N$ values across all sites, confirming its high vagility (Harvey and Kitchell 2000). Farwell (2000) examined $\delta^{13}C$ and $\delta^{15}N$ signatures in white sucker (*Catostomus commersoni*) at three sites in an undeveloped northern Ontario river over a distance of 67 km and found values differed by only 0.6‰, suggesting that the suckers were integrating their surroundings over broad spatial scales.

The prediction that ^{15}N values would be enriched in the agricultural region because of fertilizer inputs from adjacent potato fields was based on previous stable isotope research. Harrington et al. (1998) showed that $\delta^{15}N$ in Atlantic salmon parr was strongly related to the amount of agricultural land within a catchment. Hebert and Wassenaar (2001) also showed that $\delta^{15}N$ in feathers of juvenile mallard ducks were highest in regions of high agricultural development. The inconsistent finding in our study was likely due to the type of agricultural activity and the type of fertilizers applied to the fields. $\delta^{15}N$ values of animal manure range from 10‰ to 20‰, whereas synthetic commercial fertilizer has a range of 0‰ to 3‰ (Kendall 1998). The studies by Harrington et al. (1998) and Hebert and Wassenaar (2001) were both carried out in regions with livestock feedlots and manure-fertilized fields, suggesting those were the sources of enriched ^{15}N.

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That the fields in the Little River catchment are almost exclusively fertilized with synthetic commercial fertilizer blends (J-L. Daigle, Eastern Canadian Soil and Water Conservation Centre, Saint André, New Brunswick, personal communcation) may explain the lack of significant nitrogen enrichment downstream of agricultural inputs.

By contrast to ^{15}N, there was a progressive downstream enrichment of ^{13}C in sculpin muscle. Adjacent sites were most similar, with the largest difference seen between the upper forested sites and the lowermost site in the agricultural region. Doucett et al. (1996) observed similar longitudinal ^{13}C enrichment for algae and fish among sites following the stream continuum in a forested central New Brunswick stream. The authors proposed that the enrichment was due to a progressive enrichment in dissolved inorganic carbon: from ^{13}C-depleted groundwater sources in the headwaters to incorporation of ^{13}C-enriched atmospheric CO_2 in downstream regions where algal-derived carbon sources predominated in the food chain.

Slimy sculpin isotope values were stable over time, with site-specific deviations less than 0.5‰ and 0.9‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. Harrington et al. (1998) observed a similar temporal stability in $\delta^{15}N$ values of 0+ and 1+ salmon parr, with a difference of between 0.4‰–0.9‰ over 1 year. Coupled with the narrow spatial isotopic values at each site and the slow metabolic turnover rates observed in fishes (Hesslein et al. 1993; MacAvoy et al. 2001), the temporal stability provides independent evidence that the fish are probably not moving significantly within the system and are resident within a small spatial scale.

Variations in the carbon and nitrogen stable isotope content arise from food sources and accumulate in tissues of consumers as they are passed up the food web (Peterson and Fry 1987). In turn, there are many factors that can influence $\delta^{13}C$ values in food sources: from seasonal changes in primary production (Leggett et al. 1999) to differences in water turbulence (France 1995) or $\delta^{15}N$: from catchment denitrification (Kendall 1998) to anthropogenic nitrogen inputs. Numerous studies have shown that a dual-isotope approach can be a powerful and informative way to study differences between populations of animals (Harrington et al. 1998). Fry et al. (1999) described trophic relationships in a food web in Lake Okeechobee, Florida, using $\delta^{15}N$ values, but in combination with $\delta^{13}C$, habitats with site-specific isotopic signatures were differentiated over a wide variety of fish species. Wayland and Hobson (2001) used stable nitrogen and sulphur isotopes to distinguish biota from upstream or downstream of pulp mill and sewage effluents. Galloway et al. (2003) found very different $\delta^{13}C$ and $\delta^{15}N$ signatures in slimy sculpin collected downstream of effluents from a paper mill and a pulp mill but on opposite banks of the Saint John River. A distance of approximately 200 m between sites suggested that the sculpin were not moving across the river and instead were likely reflecting the conditions of the habitat in which they were collected. Isotopic differences tend to be more apparent when there is an external and unnatural source of isotopes entering the system, and such is the basis for natural tracer studies (Hershey and Peterson 1996).

In conclusion, our objective was to assess the suitability of stable isotopes as a tool to evaluate the site fidelity of slimy sculpin. With a relatively sedentary species like the sculpin, we were able to show that it is not necessary to have an anthropogenic signal to observe differences among sites on a relatively small spatial scale. There were no significant differences in $\delta^{15}N$ associated with land-use activity. This was likely due to the use of commercial fertilizers with low $\delta^{15}N$ values. Using a dual-isotope approach, we were able to identify site-specific isotopic signatures showing low spatial and temporal variation. The low variability and geographically distinct signatures suggest that the fish were displaying a high degree of site fidelity and limited instream movement. Therefore, we suggest the slimy sculpin may be a suitable fish species for environmental monitoring when residency and exposure are important factors.

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Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design

J.A. Miller and A.L. Shanks

Abstract: Although dispersal distances of marine larvae influence gene flow and the establishment of population structure, few data on realized dispersal distances exist for marine species. We combined otolith microstructure and microchemistry of black rockfish (*Sebastes melanops*) to assess their potential to provide relative estimates of larval dispersal distance. In 2001 and 2002 we measured trace elements at discrete otolith regions, representing the (*i*) egg/early-larval, (*ii*) pelagic larval, and (*iii*) late-larval/early-juvenile periods of fish collected at three locations 120–460 km apart. Discriminant-function analyses based on geochemical signatures at each otolith region accurately grouped an average of 85% (jackknife = 67%) and 87% (jackknife = 81%) of the fish to collection location in 2001 and 2002, respectively. Age at collection ranged from 83 to 174 days and parturition dates within each site were spread over a 22- to 66-day period. Therefore, individuals within sites were not released at similar times. A probable explanation of these data is that larvae from different geographic locations did not mix during ontogeny and possibly did not disperse long distances alongshore. Larval dispersal distances may be appreciably shorter, <120 km, than previously assumed based on models of passive dispersal.

Résumé : Bien que la distance de dispersion des larves marines affecte le flux des gènes et l'établissement de la structure de population, il existe peu de données sur les distances réelles de dispersion des espèces marines. Nous avons évalué le potentiel d'une étude combinée de la microstructure et de la microchimie des otolithes du sébaste noir (*Sebastes melanops*) pour estimer les distances de dispersion des larves. En 2001 et 2002, nous avons mesuré les éléments en traces à des points distincts des otolithes, représentant les périodes (*i*) embryonnaire et larvaire précoce, (*ii*) larvaire pélagique et (*iii*) larvaire tardive et juvénile précoce chez des poissons de trois sites distants les uns des autres de 120–460 km. Une analyse des fonctions discriminantes basées sur les signatures géochimiques dans chacune des régions de l'otolithe regroupe correctement 85 % (67 % après un jackknife) des poissons récoltés en 2001 et 87 % (81 % après un jackknife) en 2002. Les âges à la récolte varient de 83 à 174 jours et les dates de ponte à chaque site s'étendent sur une période de 22–66 jours. Les individus ne sont donc pas relâchés simultanément à tous les sites. Une explication probable de ces données est que les larves des différents sites géographiques ne se mêlent pas entre elles au cours de l'ontogénie et qu'elles ne se dispersent probablement pas sur de grandes distances le long du rivage. Les distances de dispersion des larves sont peut-être considérablement plus courtes, soit <120 km, que l'on estimait antérieurement d'après les modèles de dispersion passive.

[Traduit par la Rédaction]

Introduction

Information on larval dispersal distances is rare for marine species (Shanks et al. 2003). Yet dispersal distances of marine larvae affect gene flow and the geographic range and persistence of populations and species (Jablonski 1986; Sinclair 1988; Strathmann et al. 2002). The concept of a population, or "a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersive and (or) migration behavior", is integral to ecology and essential for effective conservation and management (Berryman 2002). However, the data currently available on "normal dispersive and migratory behavior" are insufficient to define realistic spatial scales for nearly all marine populations.

Obtaining accurate empirical estimates of larval dispersal distances has been hampered by inadequate analytical techniques. Individual tagging studies are expensive, logistically difficult, and typically not feasible for larval stages, during which mortality often exceeds 90% (but see Jones et al. 1999). Although genetic techniques can underestimate the extent of population structure and offer only indirect information on larval sources and dispersal distances (Kinlan and Gaines 2003; Palumbi 2003), there is evidence for popula-

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tion structure in some *Sebastes* (rockfish) species on relatively small spatial scales, i.e., from 200 to 900 km apart (Withler et al. 2001; Buonaccorsi et al. 2002; Roques et al. 2002). Such studies hypothesize that limited larval dispersal may be one mechanism contributing to the genetic divergence observed (Withler et al. 2001; Buonaccorsi et al. 2002; Roques et al. 2002).

Assumptions regarding larval dispersal in marine populations include (*i*) dispersal is primarily passive, (*ii*) dispersal distances are typically long, (*iii*) recruitment into a population comes from outside sources, and therefore (*iv*) populations are primarily open (Cowen et al. 2000). Recent empirical evidence suggests that larval retention around islands and reefs may be more common in species with planktotrophic larvae than previously believed (Scheltema et al. 1996; Swearer et al. 2002; Taylor and Hellberg 2003). The extent of self-recruitment in species with extended pelagic larval periods that reside along continental margins, however, is not known. Current management efforts, such as the establishment of marine protected areas for both maintenance of biodiversity and population-recovery efforts, are hampered by the "current paucity of information regarding meroplanktonic larval transport processes" (Lockwood et al. 2002).

Black rockfish (*Sebastes melanops*) range from the Aleutian Islands, Alaska, to southern California. Commercial and recreational harvest began in the late 1800s and continues today. *Sebastes melanops*, combined with blue rockfish (*Sebastes mystinus*) comprised over 90% of Oregon's recreational harvest in 2001 and 2002 (Oregon Department of Fish and Wildlife catch statistics). These long-lived (≤50 years) viviparous fish commonly occur in waters <55 m in depth and reach sexual maturity between 3 and 9 years of age (Cailliet et al. 2001; Love et al. 2002). Larvae and juveniles are pelagic for 3–6 months, although the areas of parturition are unknown. Benthic juveniles initially settle in shallow waters and move into deeper waters as they grow (Love et al. 2002).

Teleost otoliths grow by continuous deposition of calcium carbonate with no evidence of resorption. At the time of deposition, certain trace elements accumulate within otoliths in proportion to seawater concentration (Campana 1999; Bath et al. 2000; Elsdon and Gillanders 2003). Therefore, otolith elemental composition can reflect ambient water conditions at the time of deposition. Laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) allows elements to be measured along the otolith growth axis to provide a chronological record of trace-element deposition. Comparisons of trace-element concentrations along the growth axis of fish collected in different areas may yield information about the relative distances larvae dispersed.

Unique geochemical signatures have been documented in otoliths of marine fish collected from estuaries and along cross-shelf gradients (Gillanders 2002*a*; Swearer et al. 1999; Thorrold et al. 1998). Similarly, studies on coastal water chemistry typically focus within estuaries or along cross-shelf and depth gradients (Chester 1990; Flegal et al. 1991; Munksgaard and Parry 2001). Although there is some evidence of alongshore gradients in certain trace metals (Sañudo Wilhelmy and Flegal 1991), it is not yet clear whether, or how, otolith elemental composition varies on alongshore gradients. Trace-metal concentrations in seawater vary depending on external inputs (atmosphere and river), physical factors (upwelling, wind mixing), and biological processes (uptake and regeneration) (Cotte-Krief et al. 2002). These factors, i.e., riverine inputs, upwelling intensity, and biological community composition, vary alongshore in marine environments. Therefore, we hypothesized that there would be variation in the otolith chemistry of *S. melanops* collected along the Washington and Oregon coast.

Otolith microchemistry studies typically employ either a "top-down" or "bottom-up" approach when population structure, or connectivity (Thresher 1999), is examined. The top-down approach typically involves assaying adults across a relatively broad region and searching for geographic groupings based on otolith geochemical signatures and, in many ways, is similar to a genetic approach. The bottom-up approach involves attempting to characterize geographic source signatures in otoliths of larvae or juveniles, collecting dispersed adults at a later time, and then identifying the source of those adults by matching the chemical signatures at their otolith cores, which represent natal origins, with those previously observed in larvae and juveniles. These efforts are based on a number of assumptions. Two primary and relatively well-established assumptions are that otolith growth is continuous, with no evidence of resorption, and thus provides a permanent chronological record (Campana 1999; Thresher 1999; Campana and Thorrold 2001). The other major assumption, although not as well established, is that if fish reside in water masses with different chemical properties, those properties will be reflected in otolith microchemistry (Thresher 1999; Campana and Thorrold 2001).

In this study, we combined aspects of the top-down and bottom-up approaches. We used otolith elemental composition as a relative indicator of larval and juvenile movement. We did not attempt to identify specific larval sources. Rather, we used otolith elemental composition of *S. melanops*, a northeast Pacific species with an extended (3–6 months) pelagic larval and juvenile period, in conjunction with microstructure analyses, to determine if we could generate relative estimates of alongshore dispersal distance. To do this, we compared otolith geochemical signatures at three discrete positions along the otolith growth axis throughout the early life history of fish from different geographic locations.

The varied geology of the Washington and Oregon coast may contribute to alongshore differences in the elemental composition of otoliths in coastal fishes. Sediments from the Columbia River dominate coastal waters from Grays Harbor, Washington, to Tillamook Head, Oregon (Komar 1997) (Fig. 1). Oregon's Coast Mountain Range extends from the Columbia River southward to The Klamath Mountain Range (Orr et al. 1992). These mountains have different geologies, and the volcanic rocks are different in age and mineralogy. Alongshore differences in salinity and silicate concentrations, primarily due to freshwater discharge from the Columbia River, occur between Oregon's north and south coasts (Landry et al. 1989). In this study, we determined if the trace element composition of *S. melanops* otoliths varied alongshore and throughout the ontogeny.

Sebastes melanops larvae and pelagic juveniles are found associated with upwelling fronts but are also found landward and seaward of such fronts (Larson et al. 1994). In Oregon,

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Fig. 1. Geographic locations (underlined) where juvenile black rockfish (*Sebastes melanops*) were collected. In 2001, juveniles were collected from (*i*) the mouth of Grays Harbor, Washington (46°53′25″N, 124°06′10″W), (*ii*) Cape Arago, Oregon (43°18′10″N, 124°23′45″W), and (*iii*) Lone Ranch Beach, Oregon (42°05′55″N, 124°20′30″W). In 2002, juveniles were collected from (*i*) the mouth of Tillamook Bay, Oregon (45°33′36″N, 123°54′35″W), (*ii*) Cape Arago, and (*iii*) Lone Ranch Beach. The sites closest to each other, Cape Arago and Lone Ranch, were 120 km apart and those most distant from each other were 460 and 330 km apart in 2001 and 2002, respectively.

larval release typically occurs between February and May and juveniles are found nearshore, and occasionally in estuaries, beginning in June (Love et al. 2002). Hence, early in larval development in *S. melanops*, alongshore flow in the California Current system is predominantly poleward, owing to the Davidson Inshore Counter Current. The subsequent 3- to 6-month pelagic phase extends throughout the spring transition and the initiation of the upwelling season, when dominant flow over the shelf is toward the equator (Strub et al. 1987). If larval dispersal is widespread with extensive (>1 month) periods near the upwelling front, we predicted that otolith elemental signatures from discrete life-history periods would not be useful for discriminating fish on the basis of collection locations. If otolith elemental signatures from discrete periods classify fish to their collection location, then fish most likely stayed together relative to the other collection locations (i.e., did not mix), did not move appreciable distances alongshore, or both. Alternatively, fish collected at the same location may have followed similar dispersal pathways. Otolith-microstructure analysis provided

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information on the timing of parturition, individual age, and otolith growth to aid interpretation of otolith geochemical signatures.

Methods

The hypotheses that (*i*) the elemental signatures of *S. melanops* otoliths vary geographically alongshore and (*ii*) the elemental signatures of fish collected within sites are more similar than those of fish collected between sites were tested with juveniles collected at three locations ranging from 120 to 460 km apart in 2001 and from 120 to 330 km apart in 2002 (Fig. 1). To compare elemental signatures from various periods in the fish's life, we examined, on each otolith, three laser-ablation transects. These transects were located at (*i*) the otolith core, (*ii*) its outer edge, and (*iii*) midway between the core and the edge. The transect at the otolith core was 25 µm long, while the transects at the outer edge and midway between the core and edge were 120 µm long. Daily otolith increment widths ranged from 1 to 11 µm (average 6 µm), with smaller increment widths located in the core region. The 25 µm long transect represented, on average, the maternal incubation period plus 7 days postparturition, while each 120 µm long transect represented, on average, a 20-day period. Owing to the viviparous nature of this species, the core transect is laid down during incubation of the embryo within the mother (mean otolith radius 11.3 µm; see the section Fish collection and otolith preparation below) and very early larval stages (average otolith radius 13.7 µm). The otolith-core transect is hereinafter referred to as the "early-larval" elemental signature. The pelagic-larval period, or "larval" elemental signature, was characterized by the transect midway between the early-larval and edge signatures. The edge transect characterized the juvenile stage, or "juvenile" elemental signature.

At each sampling location, all fish were collected on the same day. Individuals collected within a site were exposed to the same water immediately prior to collection. Hence, the juvenile elemental signatures within a site may be the most similar and are most likely to yield accurate geographic classifications. If elemental signatures from the early-larval and larval periods also classify a high percentage of fish to collection location, it is probable that fish either stayed together, relative to the other collection locations, during the pelagic-larval phase, did not move appreciable distances, or both. Alternatively, fish from the same collection locations may have followed similar dispersal pathways.

Fish collection and otolith preparation

Juveniles were collected by seine in nearshore kelp beds between 14 July and 3 August 2001 and 11 and 16 June 2002. Fish were immediately measured to the nearest 0.5 mm. Sagittal otoliths were removed on the day of collection (2002) or fish were frozen (<2 months) prior to otolith removal (2001). Otoliths were removed with acid-washed plastic forceps, cleaned, weighed (to the nearest 0.01 mg), measured (to the nearest 0.1 mm), embedded, and ground to expose the otolith core. Otoliths were ultrasonically cleaned in NANOpure® water, dried, and stored in acid-washed plastic vials prior to embedding in resin. Otoliths were ground with 3M™ Tri-m-ite wetordry™ paper (240–1200 grit), polished with Buehler AlO_2 powder (12.5 and 3.0 µm), and again cleaned ultrasonically for 15 min.

Yoklavich and Boehlert (1987) validated daily otolith-increment deposition in juvenile *S. melanops*. Therefore, we were able to determine individual ages with otolith-microstructure analysis. Polished otoliths were examined under oil immersion at 1000× magnification with a Leitz Laborlux S compound microscope. Laidig and Ralston (1995) identified a dark check at the edge of the nuclear radius in juvenile otoliths of eight *Sebastes* species. Check marks were located at species-specific radii ranging from 10.93 to 16.96 µm. Ralston et al. (1996) verified, for shortbelly rockfish (*Sebastes jordani*), that the check mark was an extrusion, or parturition, check. We consistently observed a distinct check mark on *S. melanops* otoliths at a radius of 10.6–12.5 µm, with a mean of 11.3 µm. Therefore, we interpreted the check mark as a parturition mark and counted increments, each representing 1 day, from that mark to the otolith's distal edge. If a check mark was not visible, increment counts began at a radius of approximately 11 µm. Otolith counts were independently determined three times. Parturition dates were then determined for each individual. In some cases, fewer individuals were aged than were used in microchemistry studies, owing to inability to adequately discern all growth increments.

Optimas image-analysis software (version 6.0; Optimas Corporation 1996) and a Laborlux S compound microscope at 400× magnification were used to visualize and measure otolith increments within the larval and juvenile transects. A minimum of 15 otolith-increment widths were measured within each transect. No measurements were taken for the early-larval transect because of its short length and poor increment resolution. Individual and site averages were generated for the larval and juvenile transects in both 2001 and 2002. Analysis of variance (ANOVA) was used to determine if there were significant differences in increment width among locations within years.

Trace-element analysis

All LA-ICPMS work was completed at the Oregon State University's WM Keck Collaboratory for Plasma Spectrometry, Corvallis, Oregon. A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used for all analyses. The laser was set at a pulse rate of 15 Hz and a 45- and 40-µm spot ablation were used in 2001 and 2002, respectively. The small change in the ablation spot size between years was due to changes in the PlasmaLab® laser software (VG Elemental, Winsford, Cheshire, UK). The high calcium content of otoliths can cause significant buildup inside the sample chamber and quadrupole. To avoid biased data collection, background levels of ^{43}Ca were monitored for accumulation in the spectrometer, and skimmer cones and gas tubing were cleaned daily. We collected no data during a period with elevated background calcium levels.

Time-resolved software (PlasmaLab®) allowed analyte (i.e., ^{25}Mg, ^{43}Ca, etc.) measurements to be made at discrete positions on the otolith and integrated and averaged for each element collected. Preliminary data analyses indicated no difference in analyte concentrations between left and right otoliths (paired *t* tests, $n = 5$, $p > 0.20$, df = 9). Only left otoliths, however, were used in all subsequent analyses. Further

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analyses indicated no difference in analyte concentrations between transects in the different otolith quadrants (paired *t* tests, $n = 6$, $p > 0.10$, df = 9). All subsequent transects were located in the anterior dorsal quadrant and extended from the core to the otolith edge. Preliminary analyses indicated that concentrations of the following nine analytes in otoliths were well above background levels: ^{25}Mg, ^{43}Ca, ^{48}Ca, ^{55}Mn, ^{66}Zn, ^{86}Sr, ^{87}Sr, ^{138}Ba, and ^{208}Pb. The average relative standard deviation (%RSD) for National Institute of Standards and Technology (NIST) glass plates during data collection were as follows: ^{25}Mg = 11.3%, ^{43}Ca = 5.6%, ^{48}Ca = 5.6%, ^{55}Mn = 6.4%, ^{66}Zn = 8.4%, ^{86}Sr = 7.7%, ^{87}Sr = 7.3%, ^{138}Ba = 7.5%, and ^{208}Pb = 9.2%. Variation in the average %RSD between the 25- and 120-µm transects was less than 1.5%. VG PQ ExCell ICPMS minimum detection levels are 1–10 parts per trillion for Mg, Ca, Mn, and Zn and <0.1–1 parts per trillion for Sr, Ba, and Pb.

Trace-element compositions in NIST glass standards are homogeneous, and elemental concentrations are reported in Pearce et al. (1997). A NIST standard was run with each otolith sample; this allowed all otolith transects to be standardized to account for instrument drift or day-to-day variations in instrument sensitivity across the atomic-mass range. Background analyte levels were determined with an argon gas blank prior to each transect and subtracted from both mean otolith and NIST glass slide measurements. Elemental data (in counts per second) were standardized by ^{43}Ca to adjust for variability in instrument sensitivity and the amount of ablated material (Campana et al. 1997). Measured element-to-calcium ratios from NIST glass slides were then multiplied by known average NIST concentrations to generate a correction factor. Otolith element-to-calcium ratios were then multiplied by the NIST correction factor collected at the same time as the otolith measurement. Standardized ratios were transformed to attain normality and homogeneity of variance. The only case in which the variance among collection sites could not be stabilized was for ^{25}Mg (Levene's test, $F_{[2,67]} = 3.8$, $p = 0.02$) in the 2002 juvenile signatures. The removal of one outlier from Tillamook Bay (TB) (i.e., ^{25}Mg-$^{43}Ca^{-1}$ >3 standard deviations from the mean) stabilized the variance (Levene's test, $F_{[2,67]} = 2.7$, $p > 0.07$).

Statistical analysis

ANOVA was used to compare the element-to-calcium ratios among sites within each otolith region in 2001 and 2002. Quadratic discriminant function analysis (DFA) was then used to group individuals based on their elemental signatures at each otolith region. Jackknifed classifications were calculated with the removal of one observation a total of *N* times ($N = 55$ and 70 in 2001 and 2002, respectively) and averaged. The best validation of a discriminant-function classification is the assignment of new cases (i.e., those not used in the development of the original classification algorithm). Jackknifed predictions are used to provide a more realistic estimate of the ability of the predictor variables to separate groups when sample sizes are not large enough to generate two independent data sets. We also used the classification algorithm based only on the early-larval otolith signatures to predict collection location of individuals using either the larval or juvenile signatures. In this case, the larval and juvenile signatures were treated as new cases, therefore jackknifed classifications were not generated. STATISTICA® (Version 6.0; StatSoft Inc. 2002) and SYSTAT® (Version 9.01; Systat Software Inc. 1998) statistical software programs were used for the above analyses.

Results

Otolith microstructure

There was no significant difference in the total length of juveniles among sites within years (ANOVA, 2001: $F_{[2,47]} = 1.8$, $p = 0.18$; 2002: $F_{[2,69]} = 0.23$, $p = 0.79$) (Table 1). The average age of individuals and thus parturition dates, however, varied significantly among sites (ANOVA, 2001: $F_{[2,47]} = 13.3$, $p < 0.001$; 2002: $F_{[2,69]} = 24.3$, $p < 0.001$) (Table 1). The differences in age within sites ranged from a minimum of 22 days to a maximum of 66 days, therefore each site included fish of a range of individual ages and parturition dates.

In 2001, daily increment width was 7.5 ± 0.8 µm (mean ± standard deviation (SD)) during the larval period and 4.8 ± 1.6 µm during the juvenile period (Table 2). In 2002, daily increment width was 7.2 ± 0.2 µm during the larval period and 6.5 ± 0.1 µm during the juvenile period (Table 2). The only significant difference in average otolith increment width occurred during the juvenile period in 2001; increment width for Grays Harbor (GH) was significantly less than for either Cape Arago (CA) or Lone Ranch (LR) (ANOVA, $F_{[2,35]} = 24$, $p < 0.001$) (Table 2).

Otolith microchemistry

There were statistically significant differences in otolith elemental composition among sites in both years (Table 3). In both 2001 and 2002, ^{25}Mg and ^{208}Pb varied significantly among sites at all three otolith regions, while ^{55}Mn varied only during the juvenile period. ^{66}Zn, ^{87}Sr, and ^{138}Ba varied significantly among sites at one, two, or three otolith regions in 2001 (ANOVA, $F_{[2,52]} > 5$, $p < 0.05$) (Fig. 2) and 2002 (ANOVA, $F_{[2,67]} > 7$, $p < 0.05$) (Table 3). Some elements displayed intra-annual variation among otolith regions (i.e., ^{138}Ba-$^{43}Ca^{-1}$ in 2001 and 2002) (Figs. 2 and 3).

The goal of DFA is to predict group membership from a set of predictors (Tabachnick and Fidell 2001). Ideally, the analysis identifies the fewest predictors that generate the greatest discrimination. In 2001, the most accurate classification was generated using ^{25}Mg, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb, and in 2002 using ^{25}Mg, ^{66}Zn, ^{87}Sr, and ^{208}Pb. All elements included contributed significantly to the classification model ($F > 2.0$, $p < 0.01$).

The DFA based on the juvenile otolith signatures grouped 88% of the fish to collection location in 2001 (jackknife = 74%) and 88% of the fish to collection location in 2002 (jackknife = 80%; Table 4). The early-larval and larval otolith signatures accurately grouped an average of 85% (jackknife = 64%) of the fish to collection location in 2001 and 86% (jackknife = 82%) in 2002 (Table 4). However, in both years, classification success was relatively good using only ^{25}Mg and ^{87}Sr in the DFA (2001: average = 68% and jackknife = 68%; 2002: average = 77% and jackknife = 76%). The additional elements improved the overall classification success by 17% in 2001 and 9% in 2002. Overall, 67%–87% of the fish were grouped to their collection location based on

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Table 1. Sizes, ages, and parturition dates for juvenile black rockfish, *Sebastes melanops*, collected at different locations in 2001 and 2002.

(A) 2001.			
	Grays Harbor (n = 11)	Cape Arago (n = 13)	Lone Ranch (n = 10)
Size (TL; mm)			
Mean ± SE	61.0±1.4	58.6±0.9	61.4±1.5
Range	58–66	51–68	51–70
Age (days)			
Mean ± SE	153.5±3.2	117.8±2.9	133.0±3.3
Range	131–173	105–143	108–174
Collection date	3 Aug.	14 July	26 July
Parturition date			
Mean ± SE	4 Mar.	18 Mar.	12 Mar.
Range	11 Feb. – 25 Mar.	21 Feb. – 31 Mar.	2 Feb. – 9 Apr.
(B) 2002.			
	Tillamook Bay (n = 15)	Cape Arago (n = 24)	Lone Ranch (n = 23)
Size (TL; mm)			
Mean ± SE	53.4±0.6	53.2±0.5	52.8±0.6
Range	49–59	47–60	47–60
Age (days)			
Mean ± SE	113.0±1.74	108.5±1.38	98.4±1.44
Range	107–129	98–125	83–108
Collection date	16 June	11 June	12 June
Parturition date			
Mean ± SE	23 Feb.	22 Feb.	6 Mar.
Range	7 Feb. – 1 Mar.	6 Feb. – 5 Mar.	24 Feb. – 21 Mar.

Note: Ages and parturition dates were determined from otolith microstructure. TL, total length.

Table 2. Average otolith increment widths (μm) during the larval and juvenile life-history periods in 2001 and 2002.

	Larval period	Juvenile period
2001		
GH	6.7±1.3	3.0±1.3**
CA	7.6±1.2	6.2±0.8
LR	8.2±1.8	5.2±1.6
2002		
TB	7.1±1.5	6.4±1.4
CA	7.1±1.2	6.5±1.4
LR	7.4±1.3	6.5±1.5

Note: CA, Cape Arago; LR, Lone Ranch; GH, Grays Harbor; TB, Tillamook Bay. Values are given as the mean ± SD; **, statistically significant difference at $p < 0.001$.

the early-larval, larval, or juvenile otolith signatures (Table 4), which is considerably better than the prior probabilities of 38% and 33% for 2001 and 2002, respectively, based on sample size and chance alone.

For all otolith regions in both years, the first canonical factor accounted for >75% of the discrimination (Figs. 4 and 5). ^{25}Mg was the most important element in the first factor (i.e., standardized canonical discriminant function (SCDF) > 0.90). Only variables with SCDFs >0.50 will be discussed. ^{208}Pb during the early larval period in both 2001 and 2002 and the juvenile period in 2002 also contributed substantially to the first canonical factor (SCDF > 0.52). ^{87}Sr during the early-larval period in 2001 was the only other variable that contributed substantially to the first canonical factor (SCDF > 0.59). For the second canonical factor, which typically accounted for <10% of the discrimination, ^{66}Zn was the dominant variable in all cases (SCDF > 0.67) except during the early-larval period in 2001, when ^{87}Sr and ^{138}Ba each had SCDF > 0.50. In 2001, ^{138}Ba contributed substantially during the larval period and ^{208}Pb in both the larval and juvenile periods (SCDF > 0.90).

The majority of cases that were misclassified grouped with the closest geographic location. Seventy percent (33 out of 47) of the original misclassifications were placed with the closest collection location, while 61% (51 out of 84) of the jackknifed misclassifications grouped with the closest location. The second most common misclassification, in both years, was for fish from the more northerly locations (GH and TB) to group with LR fish. In both the 2001 and 2002 DFAs, LR fish were located intermediate to the other two collection locations (Figs. 4 and 5), which may account for the more frequent placement of misclassified individuals into the LR group. Furthermore, in 2001, the sample size for LR was only 10 individuals and the 95% confidence ellipses for this group overlapped extensively with those for both GH and CA, which displayed very little overlap (Fig. 4). This would contribute to both the low classification rate for LR fish as well as the misclassification of GH and CA fish to LR. In 2002, when sample sizes were larger and similar (i.e., 23–24 individuals per site), the 95% confidence ellipses displayed much less overlap, and classification success improved for all groups, especially LR (Fig. 5).

To further test the robustness of our classifications, we used a classification algorithm based on only the early-larval otolith signatures to predict collection location of individuals

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Table 3. Elements used in discriminant-function analyses (DFA) and the statistical transformations (in parentheses) used to attain normality and homogeneity of variance for different otolith regions (early larval, larval, and juvenile) in 2001 and 2002.

	2001			2002		
Element	Early-larval	Larval	Juvenile	Early larval	Larval	Juvenile
^{25}Mg ($1/^{25}Mg$)	**	**	**	**	**	**
^{55}Mn ($\log_{10}{}^{55}Mn$)	ns	ns	**	ns	ns	*
^{66}Zn ($\log_{10}{}^{66}Zn$)	ns	*	ns	**	**	**
^{87}Sr ($\log_{10}{}^{87}Sr$)	**	**	ns	ns	**	*
^{138}Ba ($\log_{10}{}^{138}Ba$)	ns	ns	*	ns	**	**
^{208}Pb ($\log_{10}{}^{208}Pb$)	**	**	**	**	**	**

Note: *, statistically significant differences among collection locations at $p = 0.05$; **, statistically significant differences among collection locations at $p = 0.01$; ns, no statistical difference. Analysis of variance was used to determine significance.

Fig. 2. The untransformed elemental ratios measured in *S. melanops* otoliths in 2001: ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb. Values are site averages (± standard error) for the early-larval, larval, and juvenile otolith regions at Cape Arago (open circles), Lone Ranch (solid triangles), and Grays Harbor (shaded squares).

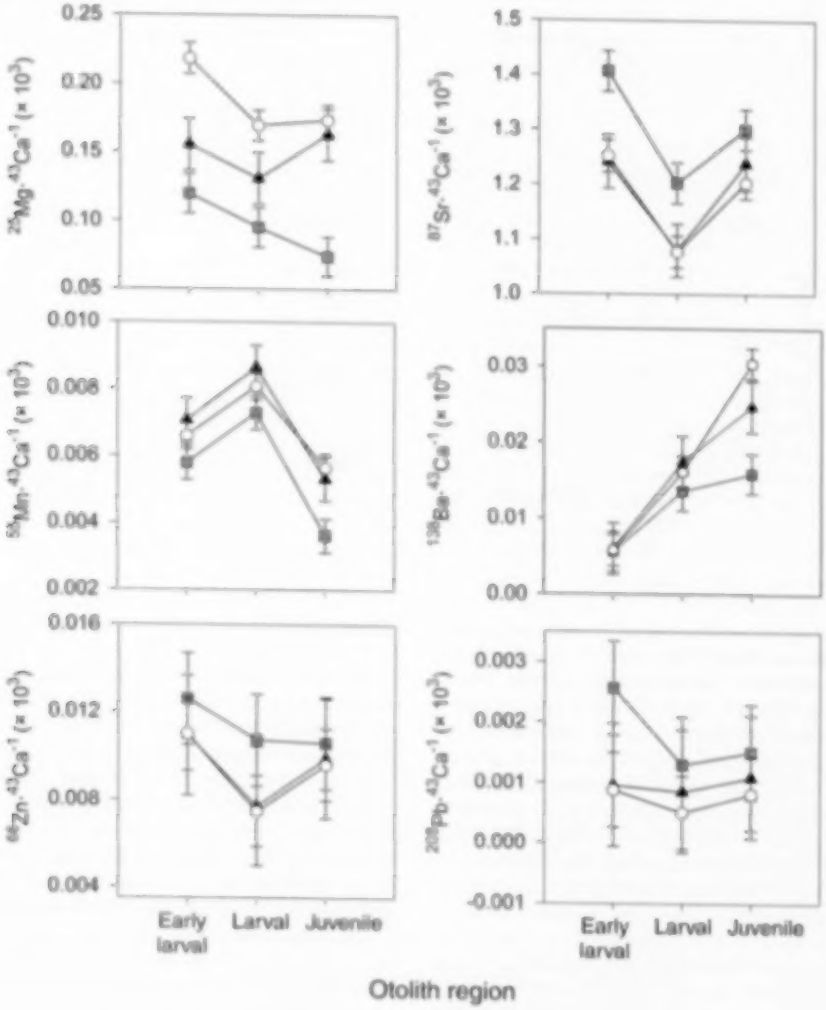

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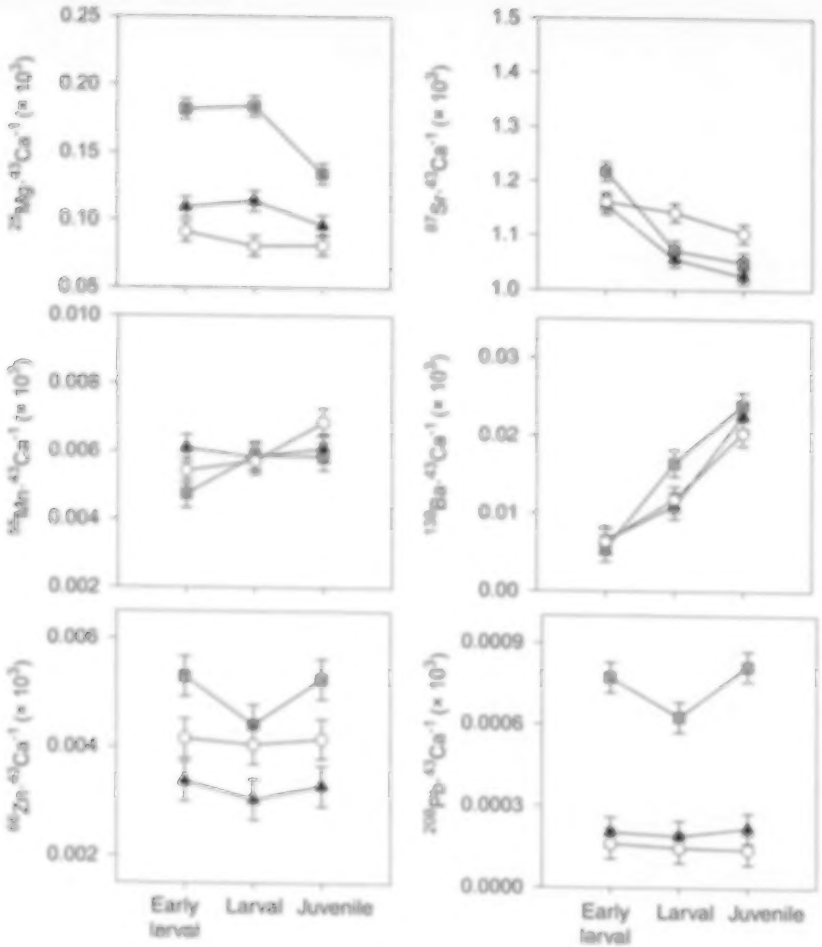
Fig. 3. The untransformed elemental ratios measured in *S. melanops* otoliths in 2002: ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb. Values are site averages (± standard error) for the early-larval, larval, and juvenile otolith regions at Cape Arago (open circles), Lone Ranch (solid triangles), and Tillamook Bay (shaded squares).



based on either their larval or their juvenile signatures. The elements used for those predictions were the same as the previous DFAs except for the removal of Ba in 2001 and Sr in 2002 because classification success was greater without them. The larval otolith signatures, using the early-larval classification algorithm, grouped 66% of the 2001 and 87% of the 2002 individuals to their collection location. The juvenile otolith signatures, using the early-larval classification algorithm, grouped 72% of the 2001 and 75% of the 2002 individuals to their collection location (Fig. 6). Misclassified individuals were most commonly placed with the nearest geographic location (i.e., 68% of misclassifications in 2001 and 62% in 2002). In 2001, the remainder of the misclassifications involved LR fish being placed in GH (25% of misclassifications). In 2002, the second most common misclassification was the placement of TB fish with LR fish (31% of misclassifications).

Discussion

We found statistically significant differences in the otolith elemental composition, including Mg, Mn, Zn, Sr, Ba, and Pb, of juvenile *S. melanops* collected on an alongshore gradient, 120–460 km apart, in both 2001 and 2002. Certain elements, such as Mg in 2001 and 2002 and Zn and Pb in 2002, varied significantly and consistently among collection locations throughout ontogeny, i.e., at all three otolith regions. The data suggest that the spatial variation in ambient water chemistry at these spatial scales was adequate to generate unique otolith geochemical signatures.

Certain characteristics of the otolith geochemical signatures observed in this study warrant further discussion. There were interannual differences in the otolith concentration of some elements (i.e., Mg and Zn) and the discriminatory power of some elements varied between 2001 and 2002

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Table 4. The percentages of *S. melanops* accurately classified to collection location based on DFAs using otolith elemental composition for different otolith regions (early larval, larval, and juvenile) in 2001 and 2002.

	Correctly assigned (%)			
Collection site	Early larval	Larval	Juvenile	Site average
2001				
GH	88 (59)	100 (76)	100 (94)	96 (76)
CA	89 (81)	89 (75)	93 (89)	90 (82)
LR	80 (40)	60 (50)	70 (40)	70 (43)
Average	86 (60)	83 (67)	88 (74)	85 (67)
2002				
TB	91 (87)	100 (91)	95 (86)	95 (88)
CA	78 (78)	88 (88)	88 (83)	85 (83)
LR	83 (78)	74 (70)	83 (70)	80 (73)
Average	84 (81)	87 (83)	88 (80)	87 (81)

Note: Values in parentheses show the jackknifed percentage correctly assigned. CA, Cape Arago; LR, Lone Ranch; GH, Grays Harbor; TB, Tillamook Bay.

(e.g., Pb was more important in the second discriminant factor in 2001). Multiyear otolith-chemistry studies have often shown that interannual variation can exceed intra-annual variation and prevent accurate classification of fish based on algorithms developed from fish otoliths collected in previous years (Gillanders 2002*b*; but see Hamer et al. 2003). Given that various factors affect coastal water chemistry, including riverine inputs and upwelling intensity, these findings are not surprising. They do, however, warrant further investigation.

Additionally, the elements most useful for discrimination varied somewhat throughout ontogeny (e.g., in 2001, Mn was more important during the juvenile life-history period). Our data are insufficient to determine whether the observed variation in elemental concentrations across the otolith represent ontogentic changes in elemental incorporation, actual changes in water chemistry, or some other, unknown factor. However, such differences may be due to temporal changes in ambient water chemistry within locations. We cannot distinguish fish movement from temporal changes in ambient water chemistry within locations. However, the fact that the geochemical signatures of the juvenile *S. melanops* otoliths grouped 60%–80% of fish to their collection location throughout their early life history does indicate that fish from different collection locations did not mix earlier in their life history. Similarly, the fact that the early-larval signatures grouped 69% and 81% of the fish in 2001 and 2002, respectively, to their collection location further suggests that fish either remained together relative to the other collection locations, did not move appreciable distances alongshore, and (or) followed similar dispersal pathways.

Thresher (1999), in an extensive review on the use of otolith elemental chemistry for resolving population structure, identified an emerging consistency in such studies. He found that the group IIA elements (Mg, Sr, and Ba) were routinely identified as stock delineators. In this study, we had relatively good jackknifed classification accuracy (68%–76%) using only Mg and Sr. Our results are consistent with Thresher's (1999) finding and indicate that otolith elemental chemistry may provide accurate information on the relative movements of individuals and groups of fish.

What transport mechanisms could have generated the otolith geochemical signatures seen in this study? We consider a number of possibilities: (*i*) fish stayed together relative to the other collection locations (i.e., did not mix); (*ii*) fish did not move appreciable distances alongshore; (*iii*) a combination of *i* and *ii*; or (*iv*) fish from the same collection location followed similar dispersal pathways. Parturition dates within each site were spread over a 22- to 66-day period. Therefore, larvae were not released at the same time. For fish from one location to remain together relative to other locations (*i*), they would have not moved appreciable distances alongshore since parturition (*ii*) or followed similar dispersal pathways for indeterminate distances (*iv*). As stated by Warner et al. (2000), when individuals in groups that settle together differ by weeks in their larval ages, any physical processes associated with accumulation over the duration of larval life must be persistent for that long. As previously mentioned, the predominant sea-surface flow in the California Current system undergoes a seasonal reversal, with predominantly poleward flow during fall and winter and equatorward flow during spring and summer (Huyer et al. 1979; Strub et al. 1987). This transition typically occurs between mid-February and mid-May, occurring later in the year at more northerly locations (Strub et al. 1987). Parturition dates of fish used in this study, i.e., from 2 February to 9 April in 2001 and from 6 February to 21 March in 2002, occurred prior to this transitional period. It is difficult to imagine what physical pathway would persist for a 22- to 66-day period in such an oceanographic regime. A more parsimonious hypothesis may be that larvae do not move appreciable distances alongshore after parturition (*ii*).

If *S. melanops* larvae did not disperse for appreciable distances alongshore during their 3- to 6-month pelagic larval period, they presumably experienced conditions conducive to reduced alongshore flow and (or) have behaviors that minimize alongshore transport. Minimal alongshore transport may occur when advective forces that promote alongshore movement are minimized relative to diffusive forces, e.g., in the nearshore coastal boundary, inshore of wind-driven "upwelling jets", and in coastal eddies. Modeling efforts indicate that coastal species which spawn over many

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Fig. 4. Discriminant-function classifications based on (*a*) early-larval, (*b*) larval, and (*c*) juvenile otolith elemental signatures for *S. melanops* collected in 2001 at Cape Arago (CA; open circles), Lone Ranch (LR; solid triangles), and Grays Harbor (GH; shaded squares). The elements responsible for most of the discrimination within each factor are identified along the axes. Ellipses are 95% confidence intervals. Group centroids (larger circles) are also plotted. Sample sizes are as follows: CA, n = 28; LR, n = 10; GH, n = 17.

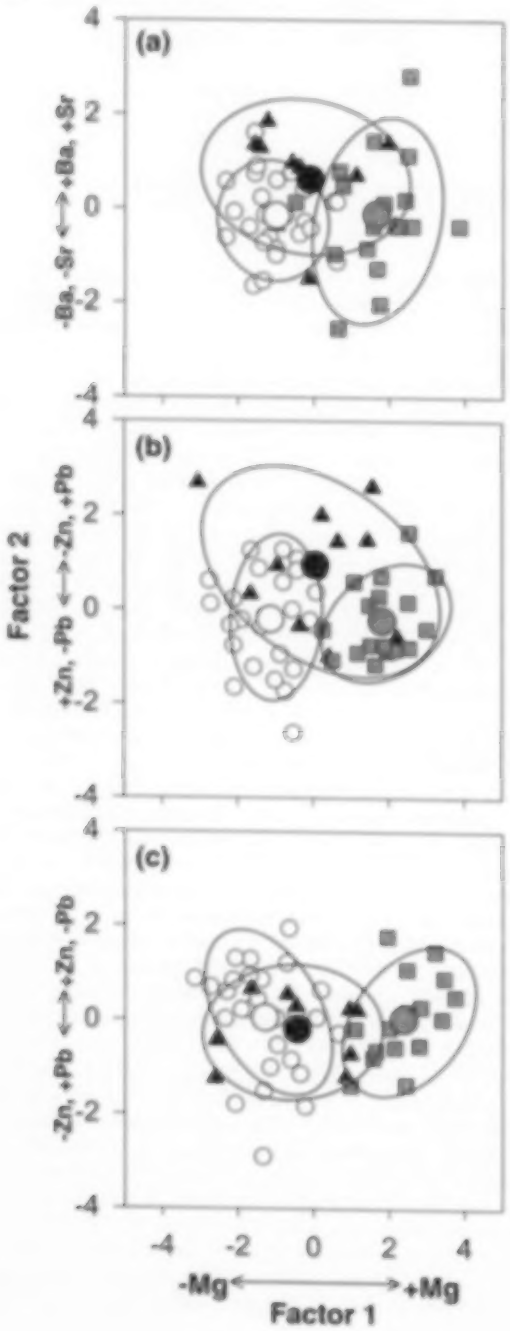

Fig. 5. Discriminant-function classifications based on (*a*) early-larval, (*b*) larval, and (*c*) juvenile otolith elemental signatures for *S. melanops* collected in 2002 at Cape Arago (CA; open circles), Lone Ranch (LR; solid triangles), and Tillamook Bay (TB; shaded squares). The elements responsible for most of the discrimination within each factor are identified along the axes. Ellipses are 95% confidence intervals. Group centroids (larger circles) are also plotted. Sample sizes are as follows: CA, n = 24; LR, n = 23; TB, n = 23.

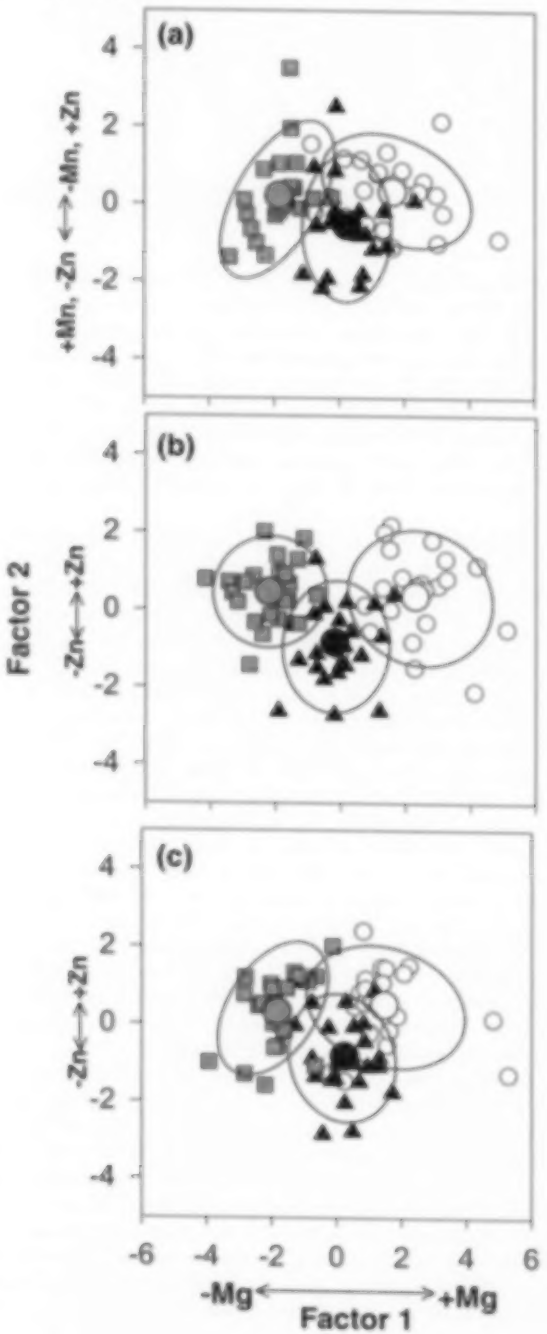

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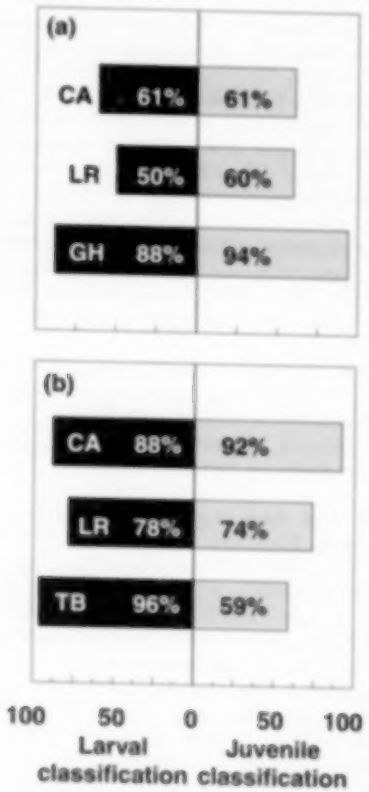
Fig. 6. Discriminant-function classification of larval and juvenile otolith elemental signatures for *S. melanops* based on the early-larval classification algorithm for (*a*) 2001 and (*b*) 2002. Bars represent the percentage of individuals grouped to their collection location based on each of the elemental signatures. Collection locations are as follows: CA, Cape Arago; LR, Lone Ranch; GH, Grays Harbor; TB, Tillamook Bay. For sample sizes see Fig. 5.



years and have extended pelagic-larval periods, two characteristics of most *Sebastes* species, are typically exposed to increased flow variability during larval stages that can, at times, result in greater diffusivity and reduced alongshore transport (Largier 2003). The reduction in alongshore transport due to physical factors could be enhanced by larval behavior (Shanks et al. 2003). Larvae may actively maintain nearshore positions with behaviors similar to those documented in intertidal fishes, including bottom orientation, rheotaxis, and schooling (Largier 2003; Marliave 1986; Montgomery et al. 1997).

Can we estimate larval dispersal distances for *S. melanops*? The closest collection locations in this study were 120 km apart. Given the rate of geographic classification at these two sites throughout ontogeny in both 2001 and 2002 (jackknife average = 63% in 2001 and 78% in 2002), these data suggest that dispersal distances may be <120 km for the majority of individuals. This may represent the dominant dispersal pattern for *S. melanops* but does not preclude the possibility that >10% of the individuals collected at a site came from distances greater than 120 km. Efforts to classify a population as "open", where recruits arrive from outside sources, or "closed", where recruits are locally derived, may not be appropriate if the long-term success of a species and maintenance of its populations depend on a variety of dispersal outcomes over time (Largier 2003).

The lack of information on larval dispersal distances and the proportion of individuals within a population that disperse widely hinders current conservation and management efforts. The maintenance of genetic diversity within a population may not be in jeopardy if >10% of the new recruits came from external sources. The recovery of a depleted population, however, depends not only on the size and proximity of adjacent populations but also on the proportion of larvae from those populations that disperse widely enough to provide new recruits to the depleted population. Therefore, recovery of such a population could be substantially slower in a species where typically 80%, compared with 20%, of the successful recruits are generated internally. Similarly, such principles apply in the design of marine reserves. Botsford et al. (2001), for example, conclude that successful reserve design requires knowledge of the mean dispersal distance as well as the proportion of successful recruits generated within the reserve. Much of the debate surrounding the design of marine reserves, i.e., whether single, larger reserves are more successful than networks of smaller reserves, will remain largely theoretically until more specific information on larval dispersal distance is generated.

Tools and techniques that provide information on larval dispersal distance and the proportion of successful recruits that are locally derived will be invaluable for the establishment of harvest regulations and conservation strategies, particularly the design and placement of marine protected areas. Otolith microchemistry has provided novel information on larval, juvenile, and adult fish movements. In this study, we found unique otolith geochemical signatures throughout ontogeny in juvenile *S. melanops* collected 120–420 km apart, which suggests that larval and juvenile movements may be relatively limited. Estimates of *S. melanops* dispersal distance based solely on the duration of the pelagic-larval period range from 255 to 570 km (Shanks et al. 2003), roughly two to five times farther than the 120 km estimated in this study. Although more information on the spatial and temporal variation in water chemistry and the relationship between ambient water and otolith chemistry is needed to fully interpret otolith geochemical signatures, the data presented here indicate that otolith chemistry holds promise in studies on alongshore fish movement and larval dispersal in coastal environments.

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Resource selection functions for age-0 Arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation

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Abstract: We developed resource selection functions (RSFs) for young-of-the-year (YOY) Arctic grayling (*Thymallus arcticus*) in a natural Barrenlands stream and used them to assess the habitat in an artificial stream created as part of a habitat compensation agreement in the Canadian Arctic. The model for small (15–21 mm) grayling explained 55% of the variation in habitat use and included water velocity, average water depth, and percentage of detritus and fines. The model for large (38–57 mm) grayling explained 36% of the variation in habitat use and included water depth, percentage of detritus and fines, and several cover variables. Model validation using a withheld sample of data indicated that the models provided good fits to the data, correctly classifying 71–75% of habitat-use locations. Applying the RSFs to observed habitat use in the artificial stream indicated an abundance of quality habitat for small grayling, but a paucity for the larger YOY. These results reflect an ontogenetic shift in habitat requirements, from the simple needs of small YOY to the more complex demands of larger YOY, demands that could not be well met by the artificial stream. We suggest that this inability contributed to the poor productive capacity of the artificial stream.

Résumé : Nous avons mis au point des fonctions de sélection des ressources (RSF) pour des jeunes ombres arctiques (*Thymallus arcticus*) de l'année (YOY) dans un cours d'eau naturel de la toundra et nous les avons utilisées pour évaluer l'habitat dans un cours d'eau artificiel créé dans le cadre d'une entente de compensation d'habitat dans l'arctique canadien. Le modèle pour les petits ombres (15–21 mm) explique 55 % de la variation de l'utilisation de l'habitat et prend en compte la vitesse du courant, la profondeur moyenne de l'eau et les pourcentages de détritus et de particules fines. Le modèle pour les ombres plus grands (38–57 mm) explique 36 % de la variation de l'utilisation de l'habitat et inclut la profondeur de l'eau, les pourcentages de détritus et de particules fines et plusieurs variables reliées au couvert. Nous avons validé les modèles en retirant un échantillon de données; les modèles s'ajustent bien aux données et classent correctement 71–75 % des sites d'utilisation de l'habitat. L'application des RSF à l'utilisation de l'habitat observée dans le cours d'eau artificiel montre qu'il y une abondance d'habitats de qualité pour les petits ombres, mais qu'il y en a peu pour les YOY plus grands. Ces résultats indiquent un changement ontogénique dans les exigences d'habitat, entre les besoins simples des petits YOY et les besoins plus complexes des YOY plus grands, des besoins qui ne pus adéquatement fournis dans le cours d'eau artificiel. Nous croyons que cette carence contribue à la faible capacité de production du cours d'eau artificiel.

[Traduit par la Rédaction]

Introduction

Much of fisheries management requires understanding the habitat requirements of species that are potentially affected by modification of habitat (DFO 1986). For many species or life stages, however, this understanding is frequently poor. Nevertheless, resource managers are often called upon to recommend, design, and implement habitat alterations without the scientific certainty they would prefer (Minns et al. 1996). Limited understanding of the relationship between fish and their habitat is particularly true in arctic regions. The need for a better understanding of fish–habitat relations, however, has never been more pressing. In the last 50 years, arctic regions have experienced a steady expansion both in the development of their natural resources and in environmental impacts (Schindler 2001). Unfortunately, these increasing pressures have not been matched by increases in research directed toward understanding arctic aquatic ecosystems or mitigating ecosystem impacts.

To provide resource managers with the information they require to evaluate habitat impacts and explore relative benefits of alternative approaches to compensation or protection,

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researchers often summarize patterns of habitat use by animals to help identify habitats considered as critical or essential (Benaka 1999). From such habitat suitability models, managers can document or predict the availability of those habitats before or after some environmental change has occurred. Overall, organisms should select habitats that provide the greatest overall gains in survival and reproduction; thus, habitat choice has evolutionary consequences (Boyce and McDonald 1999). For example, at small scales, some locations in a stream are energetically more profitable for fish than other locations (e.g., Fausch 1984; Hughes and Dill 1990). Thus, determining which habitats are selected more often than others provides fundamental information about the nature of animals and how they meet their requirements for survival.

Habitat suitability index (HSI) models, such as those published by the US Fish and Wildlife Service (USFWS 1981), range from those based on expert opinion (Delphi technique) to those developed from field data on habitat use and availability. Many HSI models are developed using a combination of approaches; however, methods are rarely tied directly to statistical estimation. For example, the only HSI model for riverine Arctic grayling (*Thymallus arcticus*) that we are aware of was developed from the authors' best estimate of habitat suitability in the absence of direct habitat use and availability of field data (Hubert et al. 1985). Regardless of their lack of empirical data or quantitative rigor, HSI models can nevertheless provide a sound basis for improved decision making and increased understanding because they specify hypotheses of habitat relationships that can be tested and improved. Aside from Hubert et al.'s synthesis, little information exists on Arctic grayling habitat selection (cf. Hughes and Dill 1990).

More recently, fish and wildlife biologists have developed a new set of methods, resource selection functions (RSFs), to describe species–habitat relationships (Boyce and McDonald 1999; Boyce et al. 2002; see also Knapp and Preisler 1999; Guay et al. 2000). Similar to HSI models, RSFs are mathematical functions that are proportional to the probability of an area being used by an animal (Manly et al. 1993). However, RSFs are statistically and quantitatively more rigorous in that they are always estimated from data (Boyce et al. 2002). In addition, RSFs can simultaneously consider multiple variables, including their interactions, and issues of spatial scale can be explored and modelled, particularly with recent advances in geographic information systems (Minns et al. 1995; Boyce and McDonald 1999).

A primary objective of the present study is to determine the habitat characteristics that influence the distribution of two size classes of young-of-the-year (YOY) Arctic grayling in an arctic stream through the development of RSFs. Following their development, we validate our grayling RSFs using a withheld sample from the same stream, i.e., we test the hypothesis that the probabilities of individual stream locations used by grayling are predictable based on these fish–habitat relationships. We then use the RSFs to assess whether habitat quality could have contributed to observed low production of grayling in an artificial stream constructed as part of a habitat compensation project. Although the artificial stream restored watershed connectivity, allowing fish migration, and provided spawning and nursery habitat for Arctic grayling, the average mass of individual YOY grayling at the end of their first summer was only 43% of the average in natural streams (Jones et al. 2003*b*). Jones et al. (2003*b*) concluded that a paucity of autochthonous and riparian-based organic matter in the artificial stream was ultimately limiting growth and production of YOY grayling; however, physical habitat also appeared to play a role worthy of investigation.

Methods

Study system

The study was centred in the Barrenlands region of the Northwest Territories, approximately 64°45′N, 110°30′W, roughly 100 km north of the tree line within the Southern Arctic ecozone (Fig. 1). At approximately 450 m above sea level, the streams of this area are the headwaters of the Coppermine, Back, and Burnside rivers, which flow north to the Arctic Ocean. Barrenland streams are generally short (380 ± 810 m; median ± standard deviation (SD)) and narrow (7.6 ± 15.1 m wide) lake-outlet systems (Jones et al. 2003*a*). Freshet begins in late May and flows (0.1–7.0 $m^3 \cdot s^{-1}$) continue until late September, when streams freeze completely. Streams can get as warm as 20 °C but average approximately 14 °C during the summer. Stream water is circumneutral, stained yellow-brown, and low in turbidity (<5 nephelometric turbidity units) and conductivity (8–19 $\mu S \cdot cm^{-1}$). Streams are used mainly for spawning and subsequently as nursery habitat for YOY grayling. In September, before the streams freeze, all fish migrate to lakes to overwinter (Jones et al. 2003*a*).

Fieldwork was conducted in Polar–Vulture stream, 700-m-long natural Barrenlands stream, and in the lower 700 m of the 3.4-km artificial stream, created as part of a habitat compensation agreement (Table 1). Since 1997, water has been diverted around two lakes, now open-pit diamond mines, through the artificial channel. The objective of the compensation was to restore watershed connectivity for fish migration and provide spawning and nursery habitats, primarily for Arctic grayling. Both the natural and artificial streams are in the same drainage system, with Polar–Vulture located approximately 2 km (and two small lakes) upstream of the artificial stream (Fig. 1). Polar–Vulture is a habitat-rich and diverse system with physical characteristics representative of many natural streams in the area (Jones et al. 2003*a*). As such, Polar–Vulture represents a reasonable regional and excellent local reference condition for comparisons with the artificial stream.

Polar–Vulture is a multichannelled stream containing a diversity of habitats for fish at several spatial scales, whereas the artificial stream consists of a single well-defined channel and rather simple habitat (Jones et al. 2003*a*; Fig. 2). In the artificial stream, blast rock lines a largely unvegetated riparian zone, whereas riparian areas of Polar–Vulture are dominated by grasses and shrubs. Aquatic vegetation common in Polar–Vulture (e.g., bur-reed, *Sparganium hyperboreum*) is very rare in the artificial stream. Age-0 grayling dominate the communities in both Polar–Vulture and the artificial stream, both numerically and by biomass (Jones et al. 2003*b*). Other species in both streams include slimy sculpin (*Cottus*

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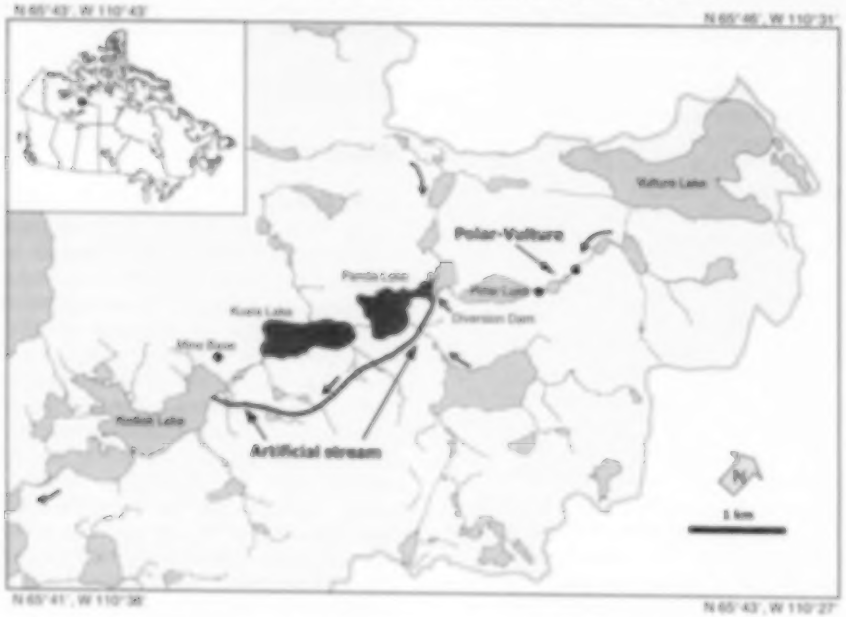
Fig. 1. Map showing the location of the artificial and Polar–Vulture streams in relation to lakes in the watershed. Koala Lake and the dark portion of Panda Lake were drained and developed as open-pit mines. Water flow, indicated by the arrows, moves from Vulture Lake to Polar Lake through the artificial stream and into Kodiak Lake. The two dots on Polar–Vulture stream indicate approximate sampling locations for that stream. Insert: location of study area in the Northwest Territories, Canada.



cognatus) and small numbers of burbot (*Lota lota*). Total densities of fish in Polar–Vulture were greater than densities found in the artificial stream in 1999, the year of this study. Paramount was that YOY grayling in Polar–Vulture were significantly larger (length and mass) than those found in the artificial stream (Jones et al. 2003*b*).

Habitat availability

Mesohabitat was classified into cascade, riffle, run, flat, and pool sequences that linearly stratify the streams into discrete units (Table 1). Microhabitat availability was quantified using stratified random sampling whereby the number of randomly assigned transects in a mesohabitat type was proportional to the length of the mesohabitat unit. Microhabitat measurements were made along randomly placed transects perpendicular to the axis of the stream. Each transect was divided into 0.5-m intervals and each interval received one randomly placed point for microhabitat measurement. At each point, we recorded average water velocity, water depth, substrate composition, distance from the nearest shore, and cover type. Water velocity was measured using a Swoffer 2100 current meter to the nearest 1 cm·s^{-1} with a top-setting wading rod 40% up from the bottom of the stream, averaged over 15 s. Depth measurements (to the nearest 1 cm) were taken from the wading rod. Percentage substrate composition within a 30-cm-diameter circle laid on the stream bottom was visually classified into clay and silt (<0.0625 mm), sand (0.0625–2 mm), small gravel (2–32 mm), large gravel (32–64 mm), cobble (64–256 mm), and boulder (>256 mm); only percent fines (detritus, clay/silt, and sand) and course (cobbles and boulders) were used for analysis. Cover types that provide velocity refuge, visual isolation, or overhead cover (sensu Fausch 1993) were estimated as a percentage of transect length and included depth, surface turbulence causing poor visibility, rock, undercut, and aquatic and terrestrial vegetation. The same methodologies were used in both streams.

Habitat use

Habitat use was determined using surface observations of YOY grayling on two occasions in each stream during the summer of 1999 (Table 2). Water clarity and relatively shallow water depths provided excellent viewing conditions. Sampling individual grayling habitat use was difficult when fish were in close proximity to each other, particularly for the small-sized YOY, early in the summer. In such cases, the group of fish was sampled as one observation. We considered a group as comprising fish using a common location with common habitat characteristics that were within 2–4 body lengths of each other. For small YOY, data were collected from the middle of the group, whereas for large grayling, data were collected from the leading fish. This difference in sampling protocol was meant to reflect the growing territorial behaviour of older and larger grayling. Fish were sampled in an upstream direction such that each grayling or group was minimally disturbed and likely only sampled once.

Once a fish or group was located, we recorded (as described above) average water velocity, total water depth, substrate composition, distance from the nearest shore, and cover type. Cover type and substrate composition was visually estimated within a 30-cm-diameter circle laid on the stream bottom. In

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Table 1. Physical and biological characteristics of Polar–Vulture stream and the lower 700 m of the artificial stream, Northwest Territories, Canada, in 1999.

Variable	Polar–Vulture	Artificial
Length (m)	700	700
Slope (%)	1.04	1.11
Sinuosity (%)	1.23	1.02
Mean width (m)	2.2 (0.75–7.0)	3.4 (0.9–5.9)
Mean depth (cm)	17 (0–85)	26 (0–87)
Mean velocity ($cm \cdot s^{-1}$)	10 (0–73)	13 (0–185)
Discharge ($m^3 \cdot s^{-1}$)	(0.07–0.02)	(0.16–0.04)
Mesohabitat composition		
Riffle (%)	43.9	1.5
Pool (%)	4.2	2.2
Run (%)	19.6	49.1
Flat (%)	19.4	3.8
Cascade (%)	1.6	33.3
Boulder garden (%)	7.2	0.0
Wetland (%)	4.1	0.0
Culvert (%)	0.0	10.1
Substrate composition		
Fines (%)[a]	20	40
Coarse (%)[b]	55	32
Grayling density (individuals·m^{-1}) in late July (mean ± SE)		
Pools[c]	3.2±0.9	0.9±0.1
Riffles[d]	5.2±1.4	2.3±0.9

Note: Numbers in parentheses represent minimum and maximum values; SE, standard error.

[a]Includes clay, silt, and sand (<2 mm).

[b]Includes cobble and boulder (>64–256 mm).

[c]Pools are slow sections of stream composed of pools and flat mesohabitats.

[d]Riffles are fast sections of stream composed of cascade, riffle, and run mesohabitats.

addition, for large grayling we measured the water velocity and depth at the lead fish's snout. The same methodologies were used in both study streams.

Differences in habitat characteristics associated with locations used by grayling versus those available were analyzed using Mann–Whitney tests. We used nonparametric testing because habitat variables were generally not normally distributed and had unequal variances that could not be reconciled using transformations.

Model development

We developed resource selection functions (RSFs) for two sizes of YOY Arctic grayling in Polar–Vulture, our reference natural stream, to describe the relationship between microhabitat characteristics and the probability of habitat use. To develop the RSFs, we used a combination of nonparametric generalized additive and parametric generalized linear models with binomial errors using S-PLUS software (MathSoft 2002). As noted by Knapp and Preisler (1999), nonparametric models relax the assumptions of ordinary linear regression in two ways: (*i*) the distribution of the dependent variable need not be symmetric homoscedasticity, and (*ii*) the relationship between the dependent and independent variables need not be linear. Relaxation of the linearity assumption between the dependent and independent variables is accomplished using a spline smoothing function (e.g., cubic B-splines) to determine the model that best fits the independent variables. Although nonparametric logistic regression is useful in describing the shape of response curves, parametric models are preferable in developing predictive models if they can provide an adequate fit to the data.

To develop the models, we first examined correlations among independent variables and excluded highly correlated variables (i.e., $r > 0.7$; Hosmer and Lemeshow 2000). We then examined each remaining variable to assess which of them had additional nonlinear effects (chi-squares, $P < 0.01$; MathSoft 2002) and plotted the response curves generated by the nonparametric regression for the significant independent variables. To develop a parametric model from the nonparametric model, we determined the appropriate generalized linear model (e.g., linear, polynomial) to approximate the nonparametric functions by examining the deviance explained between models (McCullagh and Nelder 1989). We based the final parametric model solely on the significant independent variables (analysis of variance (ANOVA), $P < 0.05$) to ensure that only those independent variables with high explanatory power were included in the model. The relative importance of each variable was evaluated by calculating the Mallow's C_p statistic (MathSoft 2002). We calculated the cumulative coefficient of determination (R^2) by adding variables to the model in the order of their associated C_p value. We also calculated the percentage that each variable contributed to the total coefficient of determination.

To evaluate the predictive success of the parametric models, we used a form of in-sample cross validation for a withheld sample of habitat-use data (Boyce et al. 2002). We used a training-to-testing ratio of 4:1, whereby model building was based on 80% of the habitat-use data, with the remaining 20% of the habitat-use data used for validation. A model with good prediction performance would be expected to correctly classify known habitat-use locations in the natural stream (i.e., locations that should have a high probability of use).

Assessment of habitat in the artificial stream

To evaluate habitat quality in the artificial stream, we used the RSFs for small and large YOY grayling developed in the natural stream to predict probability of use for both known locations of habitat use and locations considered to be available for use (taken from habitat availability surveys). For the latter, the model should predict that a relatively large number of available sites in the artificial stream would have a low probability of use and a small but unknown number of sites would have a high probability of use. We graphed the resulting distribution for the artificial stream, but caution that this is not a direct measure of habitat quality in the artificial stream. Without an independent reference against which results could be compared (Polar–Vulture could not be used as the RSF model was originally developed using availability data from Polar–Vulture), there is no context for assessment. Rather, the predicted probabilities of use of known use locations in the artificial stream are a better measure of habitat quality, as perceived by the fish. If habitat quality in the artificial stream is high, then most known habitat-use locations should be predicted to have high probability of use (i.e., at a level similar to the cross-validation procedure).

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Fig. 2. Two views of (*a* and *b*) the artificial stream and (*c* and *d*) Polar–Vulture, the natural stream.

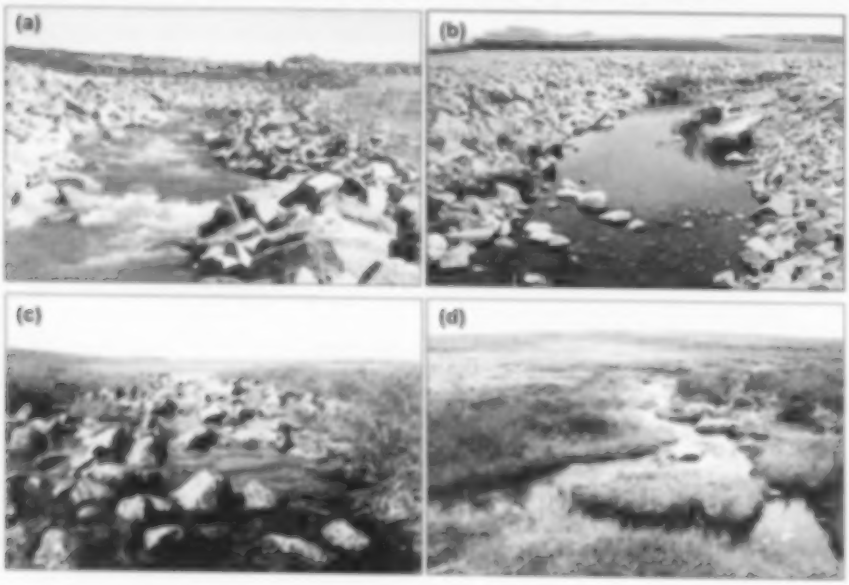

Table 2. Dates and sizes of young-of-the-year (YOY) Arctic grayling when habitat use and availability observations were made in Polar–Vulture (PV) and artificial (ART) streams in 1999.

	Small YOY		Large YOY	
Observation dates	10–15 July		13–19 August	
Stream	PV	ART	PV	ART
Number of fish total	474	1503	172	310
Solitary fish	0	1	33	74
Groups of fish	80	120	36	76
Mean group size (±SE)	5.9 (0.6)	12.5 (0.9)	3.9 (0.4)	2.1 (0.1)
Sample sizes				
Habitat use	80	121	69	150
Habitat availability (number of transects)	689 (100)	349 (43)	478 (59)	350 (47)
YOY fork length (mm)				
N	64	71	119	115
Mean (±SE)	18 (0.2)	15 (0.1)	46 (0.4)	42 (0.4)
Range	15–21	13–18	38–57	32–52
YOY mass (g)				
Mean (±SE)	0.04 (0.001)	0.01 (0.001)	0.89 (0.03)	0.64 (0.02)
Range	0.02–0.09	0.01–0.03	0.37–1.78	0.24–0.99

Note: SE, standard error; *N*, number.

Conversely, if habitat quality is low, then even most known use locations will have low probability-of-use scores based on the natural-stream RSFs. For small YOY, we used 349 random locations in the artificial stream to represent availability and 121 known use locations. For the large YOY grayling, we used 350 availability locations and 150 known use locations.

Results

Habitat availability and use: Polar–Vulture stream

For most habitat variables, YOY grayling used a narrower range than what was available in Polar–Vulture. Available and used habitats differed for all variables for small grayling (Mann–Whitney *U* tests, $P < 0.05$). Locations used by small YOY grayling were best described by shallow depths (14 cm ± 0.5 standard error (SE)) and low velocities (2 cm·s^{-1} ± 0.2 SE) in association with larger amounts of detritus (90% ± 2.3 SE) and small amounts of fine and coarse substrates. Areas used by small YOY were inevitably close to the stream banks (0.4 m ± 0.02 SE).

In contrast, locations used by the larger YOY in Polar–Vulture did not generally differ from available locations except for water depth, detritus, fines, and undercut cover (Mann–Whitney *U* tests, $P < 0.05$). Locations used by large YOY grayling were deeper (31 cm ± 1.0 SE) and contained smaller amounts of detritus (25% ± 4.1 SE) and fines (4% ± 1.2 SE) than available locations. Although not statistically

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significant, water velocities and aquatic vegetation were generally higher at sites used by large grayling than that available. These larger grayling also used locations farther out from stream banks (0.7 m ± 0.03 SE, t test = 6.05, $P < 0.001$, df = 147) than the smaller YOY.

Average snout depth of large YOY grayling in Polar–Vulture was only 11 cm ± 1.0 SE, or 35% of depth. As water depth increased beyond 40–50 cm, these grayling could be found higher off the streambed. Snout velocity, i.e., the water velocity at the fish snout, expressed as a percentage of average water velocity, varied considerably (range 0–1000%, mode 100% of average velocity) when average velocities were low (0–10 cm·s^{-1}), but was lower (median = 51%) and less variable at higher average water velocities (11–20 cm·s^{-1}).

Resource selection: small young-of-the-year grayling

The nonparametric model for small grayling in Polar–Vulture indicated that water velocity, water depth, and detritus had significant nonlinear effects ($P < 0.01$). Based on the shapes of the response curves for these three variables, we used second-degree polynomials to approximate the nonparametric functional forms. The response shapes for water depth and water velocity were hump-shaped, such that the probabilities of habitat use were maximal at 13 cm and 2 cm·s^{-1}, respectively (Fig. 3). In contrast, the probability of use increased at an accelerating rate with increasing detritus (Fig. 3).

In the final parametric model, four of the five habitat variables, the above three plus fines, had significant effects (ANOVA, $P < 0.05$) and together accounted for 55% the variance in habitat selection (Table 3). The parametric model for small YOY grayling is represented by the following equation:

$$\text{Logit line } \theta = 90.31(\text{velocity}) - 1374.77(\text{velocity})^2 - 68.20(\text{depth}) - 240.45(\text{depth})^2 + 7.89(\text{detritus}) - 4.41(\text{detritus})^2 - 7.82(\text{fines})$$

Resource selection: large young-of-the-year grayling

The nonparametric model for large YOY in Polar–Vulture indicated that four of seven of the habitat variables had significant ($P < 0.01$) nonlinear effects. Based on the shapes of these response curves, we used second-degree polynomials to approximate the nonparametric functional forms. The response shape for water depth indicated that the probability of habitat use was at a maximum at intermediate values (58 cm) (Fig. 3); similarly, the probability of habitat use for detritus and rock and aquatic vegetation cover was optimal at the intermediate values of 30%, 19%, and 24%, respectively. The probability of use for fines and cover variables depth, turbulence, and terrestrial vegetation all increased with increasing values (Fig. 3).

In the final parametric model, eight of 10 habitat variables had significant effects (ANOVA, $P < 0.05$; Table 4) and accounted for 36% the variance in habitat selection (Table 4). The parametric model for large YOY grayling is represented by the following equation:

$$\text{Logit line } \theta = 25.10(\text{water depth}) - 20.94(\text{water depth})^2 - 3.26(\text{detritus}) + 1.31(\text{detritus})^2 - 8.12(\text{turbulence}) - 15.14(\text{depth}) + 9.62(\text{depth})^2 - 1.04(\text{aquatic vegetation}) - 6.66(\text{aquatic vegetation})^2 + 9.37(\text{terrestrial vegetation}) - 33.65(\text{terrestrial vegetation})^2 + 1.51(\text{rock}) - 13.22(\text{rock})^2 + 2.64(\text{fines})$$

The in-sample cross-validation procedure for the withheld sample of data indicated that the parametric model generally performed well, correctly classifying 75% and 71% of known use locations for small and large YOY, respectively. Model predictions indicated that probabilities of use were either very high (e.g., 0.98) or very low (e.g., 0.01).

Assessment of habitat in the artificial stream

A large proportion of habitat availability sites for both small and large grayling were predicted to be used with low probability, whereas a small proportion were predicted to be used (Fig. 4). However, habitat selection by small YOY in the artificial stream indicated that the habitat quality was generally good in that a large proportion (71%) of used sites were predicted to be used with high probability (>0.9; Fig. 4). In contrast, only a small proportion (14%) of locations used by large YOY received high probability-of-use values; indeed, many locations (43%) used by large YOY in the artificial stream generated low probability-of-use values (<0.1) from the RSF (Fig. 4), suggesting that habitat quality in the artificial stream was poor.

Discussion

Ecologists frequently observe that the habitat used by an animal is only a small subset of the available habitat. As a general rule, organisms will select habitats that provide the greatest fitness (Boyce and McDonald 1999). For example, some locations are energetically more profitable than others for stream-dwelling fish (Fausch 1984; Hughes and Dill 1990), and it is generally believed that because of this, these locations have a higher probability of being used (Gowan and Fausch 2002).

Habitat profitability, however, is frequently size-dependent among stream-dwelling salmonids (Sempeski and Gaudin 1995; Nykänen and Huusko 2003). Resource selection functions indeed showed that small and large YOY grayling respond differently to available habitat. Small YOY grayling selected locations with shallow depths, e.g., near-bank and pocket-water habitats in riffles common in natural Barrenland streams. These locations were also typically in association with low water velocities related to the limited swimming ability of these small fish (Scott 1985; Gaudin and Sempeski 2001). The absence of such habitat could lead to high mortality during flooding (Armstrong 1986). As YOY grayling grow (>25 mm) and become better swimmers and increasingly territorial (Kratt and Smith 1979), they shift to the main channel where greater depths and higher mean water velocities are available. At this stage, grayling use velocity refugia associated with deep pools and created by large boulders along the thalweg from which they can feed opportunistically on drifting organisms (Fausch 1984; Hughes and Dill 1990). In contrast to small fish, habitat selection by the larger YOY thus highlights the importance of midstream cover, e.g., rocks and aquatic vegetation, that provide velocity refuge, visual isolation, and overhead cover.

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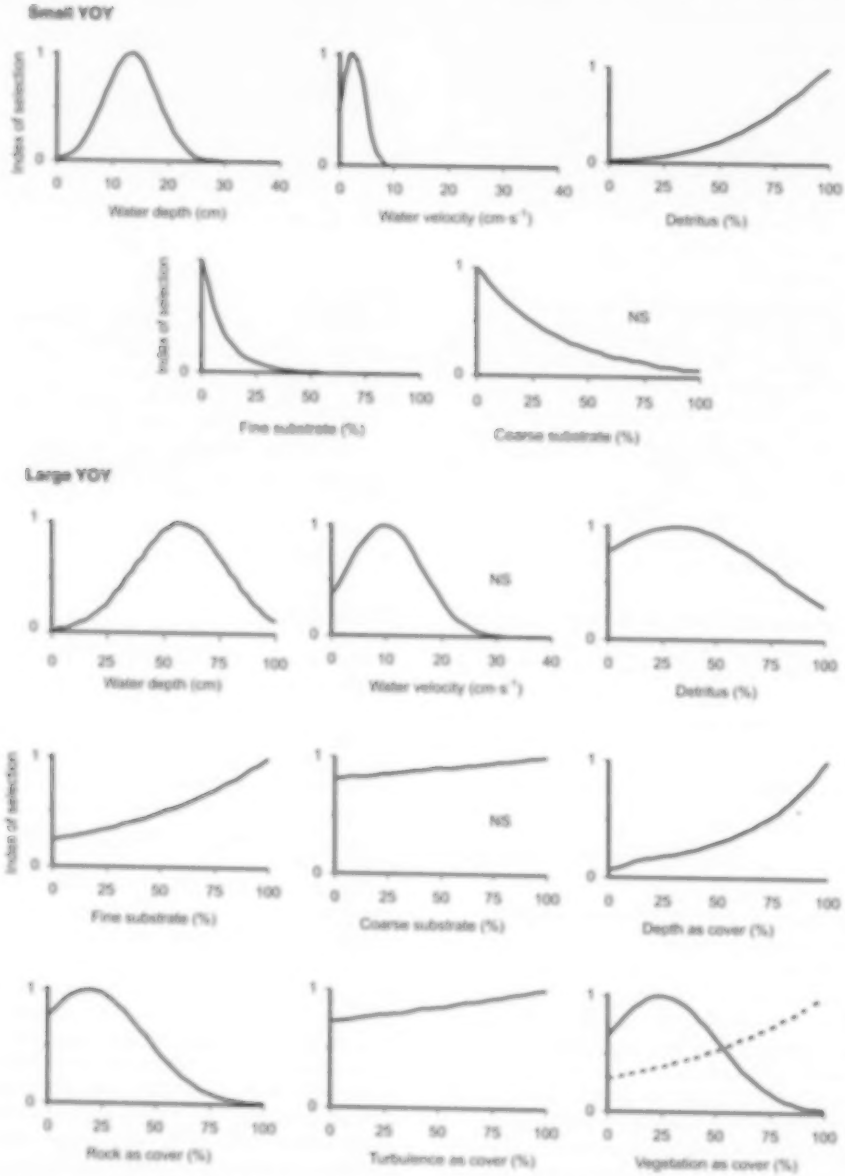
Fig. 3. Resource selection curves for small and large young-of-the-year (YOY) Arctic grayling (*Thymallus arcticus*) in a natural Barrenlands stream (Polar–Vulture). Some variables did not contribute significantly (NS) to the models. Vegetation plot (bottom right) represents aquatic (solid line) and terrestrial (broken line) vegetation. Index of selection is scaled to range from high (1) to low (0) probability of use.



Water velocity, although frequently found to be an important determinant in habitat choice by stream fishes and important for small YOY in this study, was not a significant variable in the large young-of-the-year RSF. One possible reason for this lack of statistical significance is a lack of difference between availability and use, i.e., habitat use was proportional to habitat availability. This seems unlikely given the importance of velocity refugia (Fausch 1984, 1993). We suggest that velocity refugia created by boulders, common in Barrenland streams, bias the measurement of average water velocity. In contrast to other studies, we found that snout velocity was generally some fraction of average water velocity at locations used by large YOY grayling, particularly at higher water velocities, suggesting the importance of velocity refugia to habitat selection. As such, average (i.e., depth-averaged) water velocity may be a poor measure of actual habitat availability, which may also hold true depth-averaged hydraulic models (Ghanem et al. 1996; Guay et al. 2000).

Similar to snout velocity, snout depth was typically a small fraction of total water depth. The relationship between snout and water depth increased proportionately until a water depth

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Table 3. Analysis of deviance table showing the statistical significance (P value) and R^2 values of the independent variables in the parametric logistic regression model for small young-of-the-year Arctic grayling in Polar–Vulture stream, a natural Barrenland stream.

Habitat variable	Deviance explained	df	P	Cumulative R^2	Percent of R^2
Water velocity	126.8	725	<0.0001	25	45
Water depth	91.1	723	<0.0001	43	32
Detritus	58.0	721	<0.0001	54	21
Fine	5.5	720	0.0187	55	2

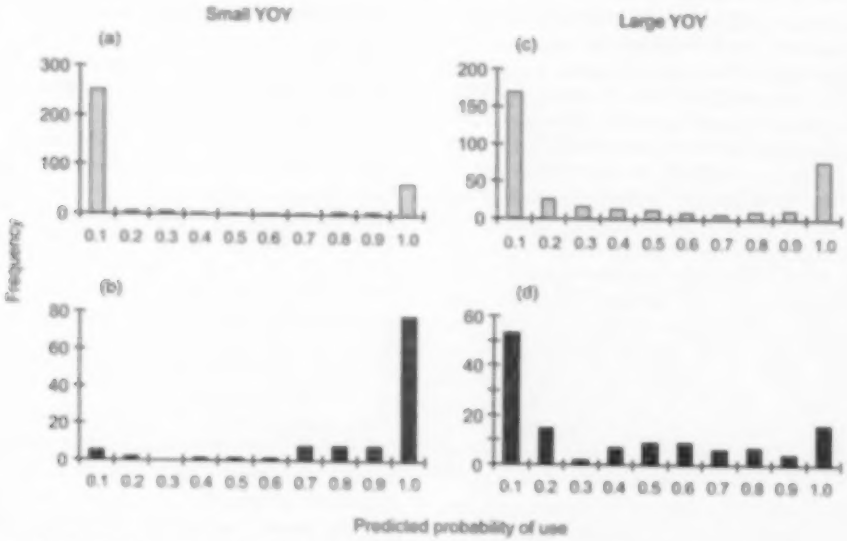
Note: Percent of R^2 is the percentage that each variable contributed to the total coefficient of determination. Italics indicate variables that had significant nonlinear effects. Null model residual deviance was 512 with 727 degrees of freedom (df).

Table 4. Analysis of deviance table showing the statistical significance (P value) and R^2 values of the independent variables in the parametric logistic regression model for large young-of-the-year Arctic grayling in Polar–Vulture stream, a natural Barrenland stream.

Habitat variable	Deviance explained	df	P	Cumulative R^2	Percent of R^2
Water depth	55.9	545	<0.0001	13	36
Detritus	25.4	544	<0.0001	19	16
Turbulence	20.0	542	0.0001	24	13
Depth	15.6	540	0.0004	27	10
Aquatic vegetation	14.8	538	0.0006	31	10
Terrestrial vegetation	12.2	536	0.0022	34	8
Rock	6.3	535	0.0419	35	4
Fine	4.2	533	0.0403	36	3

Note: Percent of R^2 is the percentage that each variable contributed to the total coefficient of determination. Italics indicate variables that had significant nonlinear effects. Null model residual deviance was 426 with 547 degrees of freedom (df).

Fig. 4. Predicted probability of use for habitat that was (*a*, *c*) available to and (*b*, *d*) used by small and large young-of-the-year (YOY) Arctic grayling (*Thymallus arcticus*) in the artificial stream, based on resource selection functions from the natural Barrenland stream (Polar–Vulture).



of 40–50 cm was reached. At that point, grayling could be found relatively higher off the stream bed, which suggests that some threshold of predator avoidance is reached due to water depth or perhaps clarity, after which grayling can move further off the bottom with little increased risk of predation from, e.g., birds.

The relative unimportance of substrate characteristics, which are often important in other studies (e.g., Knapp and Preisler 1999), was surprising. However, Barrenland streams are generally stable, permafrost-bound, and boulder-dominated colluvial systems, i.e., fluvial process are relatively ineffective at removing material deposited on the valley floor. As a consequence, substrates in Barrenland streams are poorly sorted in comparison to alluvial streams, where sorting produces a correlation between velocity and substrate (Morisawa 1968). Another reason for the limited importance

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of substrate in the RSFs may be that selection of a location does not reflect the substrate composition at that location, per se, but the substrate of an area upstream that supplies the drifting macroinvertebrates upon which grayling feed (Jones et al. 2003*c*). Thus, selection of habitat by primarily foraging YOY fish will differ from selection by spawning stream fishes, where the characteristics of substrate at a site are critical to the development and survival of eggs (Chapman 1988; Knapp and Preisler 1999).

Cover-related habitat variables, including water depth, aquatic and terrestrial vegetation, rock, and water turbulence, were important determinants of habitat use by larger YOY grayling in Polar–Vulture. Structures that provide velocity refuge allow fish to hold low velocity positions adjacent to faster water currents and thus maximize their energy intake from drifting food items while minimizing the cost of swimming to maintain position (Fausch and White 1981; Fausch 1984). Structure may also provide visual isolation, decreasing energetically costly agonistic behaviour and allowing for higher fish densities, consistent with what we observed in Polar–Vulture (Jones et al. 2003*b*). Overhead cover can decrease the amount of energy invested in vigilance against predators. As expected, the probability of habitat use typically increased with increasing cover. Unexpected was the hump-shaped form of selection for rock and aquatic vegetation. Grayling often selected a combination of cover types, with no one type being dominant. However, some cover types likely serve more than one function. For example, aquatic vegetation type can likely provide overhead cover, visual isolation, and velocity refugia.

Model validation

Ideal models for habitat selection would incorporate all of the important characteristics of fish habitat use (realism), account for a large percentage of variation in habitat use (precision), and be based on years of data from a broad geographic range to incorporate environmental variation (generality). Simultaneously maximizing all three of these characteristics in biological models is always difficult (Levins 1966) but is more so in the arctic. Nevertheless, resource managers are frequently charged with the task of evaluating changes to stream habitat in a timely manner, often in the absence of site-specific data. It is not logistically and economically possible, however, to develop resource selection functions, case by case, for all environmental conditions that may influence fish habitat use (Mäki-Petäys et al. 2002). As a result, models must be used to predict the effects of modification in systems other than those for which they were developed. Predictive power usually decreases when models are tested in novel environments. Differences in habitat availability alone may affect habitat selection, particularly if the spectrum of habitat types examined is limited. A habitat may become used more as it becomes more available, similar to a functional response (Boyce et al. 2002). To further complicate prediction, habitat use may be affected by other factors, such as food availability, competition, predation (e.g., Fausch 1984; Orth 1987; Biro et al. 2003), water temperature and season (Mäki-Petäys et al. 1997), time of day (Johnson and Covich 2000), and discharge (Holm et al. 2001). Despite these difficulties, the transferability of habitat criteria for Atlantic salmon (*Salmo salar*) was conceivable on regional and possibly "universal" scales (Mäki-Petäys et al. 2002). Although we did not examine transferability at either of these scales, it was encouraging to note that both RSF models were good predictors of habitat use, as demonstrated by the cross-validation results in Polar–Vulture. This level of predictability is noteworthy considering that group membership is uncertain when using habitat availability and use data, i.e., use is a subset of availability and thus not unique, unlike used-versus-unused habitat designs (Manly et al. 1993; Boyce et al. 2002). As a result, the strength of relationships in this study could actually be muted.

Assessment of habitat in the artificial stream

As part of a larger objective to evaluate the effectiveness of the artificial stream as habitat compensation (see Jones et al. 2003*b*), we used the RSFs for small and large YOY grayling from the natural stream to assess the quality of nursery habitat in the nearby artificial stream. Our assessment differed depending on the size class of grayling examined. Because many locations in the artificial stream where we observed small YOY grayling were, in fact, predicted by our RSFs to have a high probability of being used, we conclude that the artificial stream provides a physical environment that is comparable to that of the natural stream. In contrast, many locations where we observed large YOY were predicted to have low probability of use. Although these different results can be explained within the context of an ontogenetic shift in habitat requirements of YOY grayling, we suggest that they also reflect the poor habitat quality of the artificial stream for the larger YOY. This, along with lower temperatures and a paucity of organic energy for grayling, likely contributes to the stream's poor productive capacity relative to natural streams, including Polar–Vulture (Jones et al. 2003*b*).

Habitat requirements of small YOY are relatively simple and thus more easily met than those of the larger YOY, which could account for the differences in predicted habitat quality. As indicated by their RSF model, small YOY select shallow, slow-moving water with high amounts of detritus. They did not appear to use any cover; instead, they distributed themselves into small schools as a basic antipredation tactic. The RSF for larger YOY, explaining a lower proportion of the variance in habitat use despite more variables being included into the model, suggests that their habitat requirements are more complex. For example, territoriality and the use of various forms of cover were evident in habitat selection by larger grayling (Kratt and Smith 1979; N. Jones, personal observation).

The average mass of YOY grayling at the end of summer (1998–2001) was 57% lower in the artificial stream than in a number of natural streams (Jones et al. 2003*b*). This large difference in growth, in concert with differences in YOY grayling density, resulted in even larger differences in end-of-season standing crop between streams (Jones et al. 2003*b*). Although we previously emphasized that low amounts of allochthonous organic matter in the artificial stream limited the artificial stream's productive capacity (Jones et al. 2003*b*), we had also suggested that limited quality physical habitat likely contributed. Our results here strongly support that suggestion and identify in particular a failure of the artificial stream to provide habitat for larger YOY grayling, in-

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cluding velocity refugia, visual isolation, and overhead cover. There remains the possibility that the RSF developed for large YOY grayling in Polar–Vulture simply does not transfer to other streams, including (or especially) the artificial stream. The apparent success of the RSF for small YOY, however, argues against that alternative.

This study is the first to quantitatively measure and model habitat use and selection by YOY Arctic grayling and, given their importance in Barrenland streams (Jones et al. 2003*a*), represents a much-needed addition to the understanding of fish–habitat relations in the Arctic, a region undergoing rapid development and change. The resource selection functions proved valuable as a habitat assessment technique, showing that larger YOY were forced to use habitat that they would not normally use in the natural stream. The artificial stream restored watershed connectivity for fish migration and provided suitable spawning areas, but nursery habitats are poor, particularly with regards to the production of larger YOY grayling (Jones et al. 2003*b*). Although we could not use it directly as an assessment approach, we suggest that analyses of habitat availability using RSFs could be very useful if the results are placed in the appropriate context, using references (e.g., before vs. after a manipulation, upstream vs. downstream of an impact, or involving assessment among a group of streams).

The application of these models in the context of habitat management remains challenging, particularly in the dynamic environments of lotic habitats, which supports application of the precautionary principle. The use of these RSF models, together with geographic information systems and river flow models, such as physical habitat simulation (PHABSIM; Bovee 1986) and two-dimensional flow models (Ghanem et al. 1996), not only represents interesting ecohydraulic links, but also offers much opportunity for developing defensible methods for fish habitat assessment in rivers (e.g., Minns et al. 1995; Guay et al. 2000).

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The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data

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Abstract: We analyse the population dynamics of Northeast Arctic cod (*Gadus morhua*) by applying statistical population models to 22 years of research survey data on abundance, length, and maturation. The models for abundance and individual length are selected using Akaike's information criterion (AIC_C). Survival of 2- to 4-year-old cod was found to be negatively related to the abundance of cod relative to its preferred prey, capelin (*Mallotus villosus*), likely the result of increased cannibalism from older cod when there is a lack of capelin. Growth up to age 4 decreases with abundance and increases with sea temperature and the North Atlantic Oscillation index, whereas growth from age 4 to age 8 decreases with increasing cod–capelin ratio. The statistical models were combined in a dynamic age-structured model, coupling the dynamics of abundance and body length (reproduction depends on body length, and length growth is influenced by abundance). Simulations using this model are able to recreate the main abundance patterns of each age group for 1982–2002. The model's ability to predict changes in the abundance of spawners appeared to be most limited by our ability to predict survival of 3- to 6-year-old immature cod.

Résumé : L'utilisation de modèles statistiques de population basés sur des données d'abondance, de longueur et de maturation récoltées pendant 22 années d'inventaire nous a permis d'analyser la dynamique de la population de morues franches (*Gadus morhua*) du nord-est de l'Arctique. Les modèles basés sur l'abondance et les longueurs individuelles ont été sélectionnés d'après le critère d'information d'Akaike (AIC_C). La survie des morues de 2–4 ans est en corrélation négative avec le rapport de l'abondance des morues sur celle de leurs proies préférées, les capelans (*Mallotus villosus*). La raison probable de ce phénomène est l'augmentation du cannibalisme par les morues plus âgées lorsqu'il y a une pénurie de capelans. La croissance jusqu'à l'âge de 4 ans est fonction inverse de l'abondance; elle augmente avec la température de la mer et l'indice d'oscillation nord-atlantique. La croissance de 4 à 8 ans décline avec l'augmentation du rapport morues–capelans. Les modèles statistiques ont été couplés à un modèle dynamique structuré d'après l'âge, ce qui a permis de relier la dynamique de l'abondance et celle de la longueur du corps (la reproduction dépend de la longueur du corps et la croissance en longueur est influencée par l'abondance). Des simulations faites avec le modèle réussissent à recréer les principaux patterns d'abondance des différentes classes d'âge de 1982 à 2002. La capacité du modèle à prédire les changements dans l'abondance des reproducteurs semble être limitée surtout par notre incapacité à prédire la survie des morues immatures d'âges 3–6.

[Traduit par la Rédaction]

Introduction

It has long been recognized that to fully understand the population dynamics in marine fish, one needs to consider variation in survival and growth on all stages of the life cycle (Rothschild 2000). Nevertheless, following the pioneering work of Hjort (1914), studies of marine fish have to a large degree focused on the variance in recruitment and year-class strength. There is no doubt that abundance at metamorphosis generally is correlated with abundance at maturation (Bradford 1992; Leggett and Deblois 1994). However, the focus on the early larval stages is probably also in part due to a general lack of reliable data on survival throughout the life of the fish. Here, we analysed the variation in reproduction, abundance, and length throughout the life of Northeast Arctic (NEA) cod (*Gadus morhua*) in the

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Barents Sea, presently the world's largest stock of Atlantic cod (Worm and Myers 2003). Our analysis uses data acquired from 22 years of scientific research surveys. In contrast to virtual population analysis (VPA), survey data can be used to assess the variation in natural mortality. In traditional VPA, the natural mortality M (defined as the mortality not caused by fishing) is assumed to be a constant value (for instance, $M = 0.2$). In some cases, there is information on the variation in certain components of natural mortality, as in the case of cannibalism in NEA cod since 1984 (ICES 2002*a*), which can then be used to let M vary in the VPA analysis. However, because fish abundance is estimated by making assumptions about the natural mortality M, such estimates may therefore not be used to estimate M (if one tries, only the original assumptions are returned). In our case, the survey data is based on trawling and acoustic measurements; hence, no assumptions are made about natural mortality. On the other hand, trawl survey data are essentially catch-per-unit-effort (CPUE) data and are influenced by catchability (the proportion of fish inside the area swept by the trawl that are caught), which vary as a function of age and density. Also, the distribution area of the fish may be incompletely covered.

The overall purpose of this study was to use survey data to analyse how survival and individual growth at each age, as well as reproduction, vary with biotic factors (competition, cannibalism, prey abundance), abiotic factors (sea climate), and fishing. We did this by selecting the statistical models that could best explain abundance and length as a function of various variables related to these factors. Finally, we wanted not only to check the fit of our statistical models, but also to explore how well we can understand the dynamics of NEA cod during the 1980s and 1990s using simulations of such models. This could also be used to assess which aspects of the life history (reproduction, early survival, or late survival) provide a better understanding of the variations in the spawning stock.

Methods

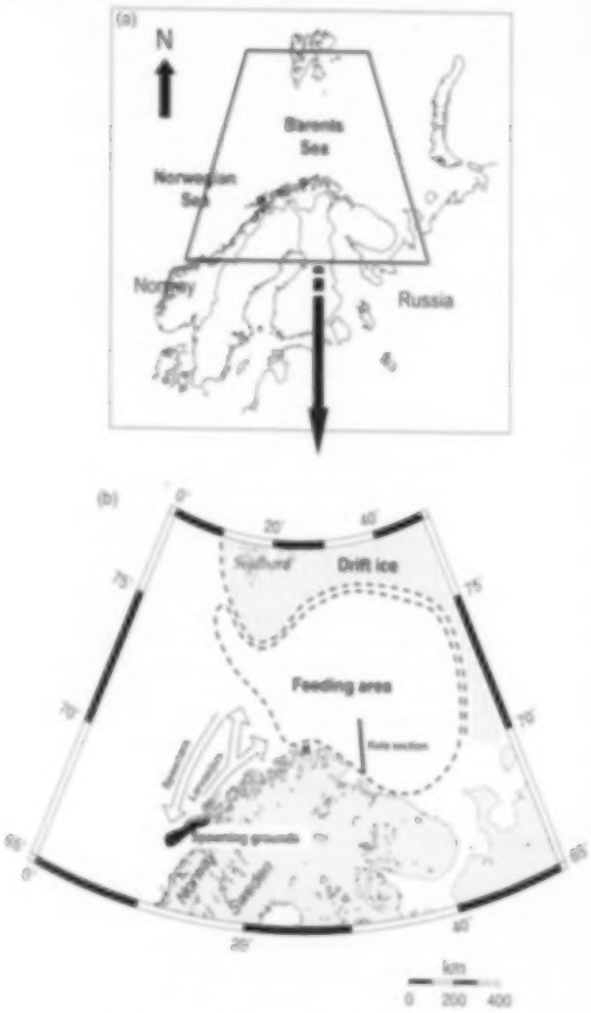
The stock

NEA cod currently mature at 6–7 years of age (Nakken 1994) and migrate out of the Barents Sea to spawn along the Norwegian coast in March to May (Bergstad et al. 1987; Fig. 1). Eggs and larvae are carried by currents into the southern Barents Sea and south and west of Svalbard (Fig. 1), and the larvae settle towards the bottom at age ~5 months. The immature cod make seasonal migrations, the extent of which increases with age. At an age of 3–4 years, capelin (*Mallotus villosus*) become a major food item, and the cod follow the spawning migration of capelin to the coasts of northern Norway and northwestern Russia in spring (Nakken 1994). Growth in length has been found to be affected by the abundance of capelin (Bogstad and Mehl 1997).

Data

The study is based on age-specific estimates of abundance and mean length derived from annual bottom trawl sampling in the winter feeding area of NEA cod in 1981–2002. The survey followed a stratified random design in 1981–1990

Fig. 1. (*a*) Scandinavia and northeastern Russia with the study area (*b*) indicated. (*b*) The winter feeding area, the annual "upstream" spawning migration of cod in January, and the "downstream" movement of larvae and juveniles from the spawning grounds to the feeding area in April–May. The Kola section, where sea temperatures are measured, is also shown in the map. The areas of drift ice and feeding vary from year to year; only their approximate extent is shown here.



and a stratified systematic design from 1991. Although the total area covered varied from 87 000 to 187 000 km^2, most cod individuals in years with a large-area coverage were sampled in the region covered in all years 1981–1999 (86% in 1999). The area was divided into plots of ½° latitude × 1° longitude, and one bottom trawl sample was taken from each plot. A Campelen 1800 shrimp trawl with 80-mm mesh size in front was used until 1993, with a codend of 35- to 40-mm stretched mesh size. The mesh size was reduced to 22 mm in 1994 (this was taken into account in the analysis, cf. Table 1). Although pelagic samples are also taken, we only used estimates from the bottom trawling in the present re-

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Table 1. Explanatory variables considered for model components (*X*s in eqs. 1 and 3).

Variable (X)	Definition	Evaluated for
Temp_{t-1}	Sea temperature, average 0- to 200-m depth in the Kola section (Bochkov 1982; Tereshchenko 1996)[a]	$N_t^1 - N_t^4$, $L_t^1 - L_t^4$
NAO_{t-1}	North Atlantic Oscillation, winter (December–March) index (Hurrell et al. 2003; see also Stenseth et al. 2003)[b]	$N^1 - N^4$, $L^1 - L^4$
Capbm_{t-1}	log(capelin biomass)[c]	$N_t^1 - N_t^8$, $L_t^3 - L_t^8$
CodCap_{t-1}	$(\log(N^5) + \log(N^6) + \log(N^7) + \log(N^8))/\text{Capbm}$[c]	$N_t^1 - N_t^8$, $L_t^3 - L_t^8$
Harvest_{t-1}^a	(Number of cod landed, age a)/N^a (a = 3–10)	$N_t^3 - N_t^{10}$
$\text{Harvest}_{t-1}^{5-10}$	(Number of cod landed, ages 5–10)/($N^5 + N^6 + N^7 + N^8 + N^9 + N^{10}$)	$N_t^5 - N_t^{10}$
N_t^4	An index of spawning success/effort in year $t - 1$	$N_t^6 - N_t^{10}$
Year_t	The year (as a continuous variable) to account for trends	$N_t^1 - N_t^4$, $L_t^1 - L_t^4$
Mesh_{t-1}, Mesh_t	Mesh = 0 for 1981–1993; Mesh = 1 from 1994 onwards[d]	$N^1 - N^2$

Note: Harvest numbers were taken from table 3.8 in ICES (2002*a*), and capelin biomass was taken from table 4.3.2.2 in ICES (2002*b*).
[a]Position: 33°30′E, 70°30′–72°30′N. Recent temperatures have been kindly provided by PINRO, Murmansk.
[b]Based on the difference of normalized sea level pressure between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland. Available from the web site of Jim Hurrell, National Center for Atmospheric Research, Boulder, USA (http://www.cgd.ucar.edu/~jhurrell/nao.html).
[c]Most of the capelin biomass is eaten by cod in the age range of 3–6 years.
[d]The mesh size was reduced in 1994 to increase the catchability of age-1 cod.

port (which accounts for >99% of the sampled fish). The coverage of the Russian Economic Zone was incomplete in the years 1997 and 1998 (for political reasons), but the estimates were adjusted in an attempt to correct for this. The number of cod (divided into 5-cm length groups) in each plot was calculated on the basis of trawling distance and effective fishing width. The Barents Sea was then divided into 4–7 larger areas (4 in 1981–1992, 7 in 1993–1999), and the age distribution for each length class was calculated for each area by estimating the age (using otoliths) for subsamples (~10%) of the trawl samples. In 1999, 265 plots were sampled, the lengths of 22 971 cod were measured, and 2321 cod were aged (Mehl 1999).

We use L_t^a to denote the estimated mean length for cod at age a in year t. These data, estimated as described above, were taken from table A6 in ICES (2002*a*). We assumed the proportion of matures in each age group, P_t^a, to vary as a logistic function of the age group's estimated mean length:

$$(1) \qquad P_t^a = \exp(\alpha + \beta L_t^a)[1 + \exp(\alpha + \beta L_t^a)]^{-1}$$

We estimated the parameters of this function by logistic regression of the observed proportion of matures as given by table 3.13 in ICES (2002*a*).

For the age classes with no mature individuals (age ≤4 years), we used the estimates of cod in the Barents Sea, estimated as described above, as given in tables A3 and A6 in ICES (2002*a*) for the total estimated number of individuals at age a in year t (hereafter denoted N_t^a). For age classes with some mature individuals (age >4 years), the total abundance could not be estimated without taking into account that mature cod are not present in the Barents Sea at the time of sampling, as they start their annual migration to the spawning grounds in December–January and return to the Barents Sea in May (Bergstad et al. 1987). We had two options to estimate the total abundance of cod, N_t^a. Either (1) we could calculate it from the relationship $N_t^a = N_t^{a,\text{imm}}(1 - P_t^a)^{-1}$, where $N_t^{a,\text{imm}}$ is the estimated abundance of immature fish in the Barents Sea or (2) we could add the Barents Sea data and acoustic estimates of the number of mature cod at the spawning grounds in Lofoten (table A4 in ICES (2002*a*)). We found that for ages 5–8, method 1 yielded the lowest interannual variance in N_t^a. For ages 9 and 10, P_t^a is close to 1, and we found method 2 to yield more reliable estimates with a lower variance. For N^{10}, we used the estimate of age 10 and older cod (the 10+ group). In all years except one, the 10+ group comprised less than 7% of individuals of the spawning stock.

Population model

We used log-linear models for abundance, a model form with good theoretical and empirical support (Royama 1992; Bjørnstad et al. 1995; Stenseth et al. 1999). This gives the following statistical models for abundance:

$$(2a) \qquad \log(N_t^1) = a_1 + (1 - b_1)\log(N_{t-1}^{\text{mature}}) + c_{1,1}X_{t-1}^1 + c_{1,2}X_{t-1}^2 + \ldots + \varepsilon_{N_t^1}$$

$$(2b) \qquad \log(N_t^2) = a_2 + (1 - b_2)\log(N_{t-1}^1) + c_{2,1}X_{t-1}^1 + c_{2,2}X_{t-1}^2 + \ldots + \varepsilon_{N_t^2}$$

$$\vdots$$

$$(2j) \qquad \log(N_t^{10}) = a_{10} + (1 - b_{10})\log(N_{t-1}^9) + c_{10,1}X_{t-1}^1 + c_{10,2}X_{t-1}^2 + \ldots + \varepsilon_{N_t^{10}}$$

The *b*s denote density-dependence when the real *N*s are known or the correlation between abundance and catchability is constant. In our case, this correlation decreases with age (Godø et al. 1999), which also affect the *b*s. The *X* terms denote effects of biotic and abiotic variables such as climate, abundance of prey, etc. For each age, a set of potential *X*s were selected based on prior knowledge of cod ecology (Table 1). We then used linear regression to select the set of *X*s that gave the optimal fit to the data (see below). Maturation in NEA cod (as in many other marine fish species; e.g., Rijnsdorp 1993) depends on length rather than on age, especially for the youngest spawning age classes. We used the following formula for the number of matures (N^{mature} in eq. 2*a*):

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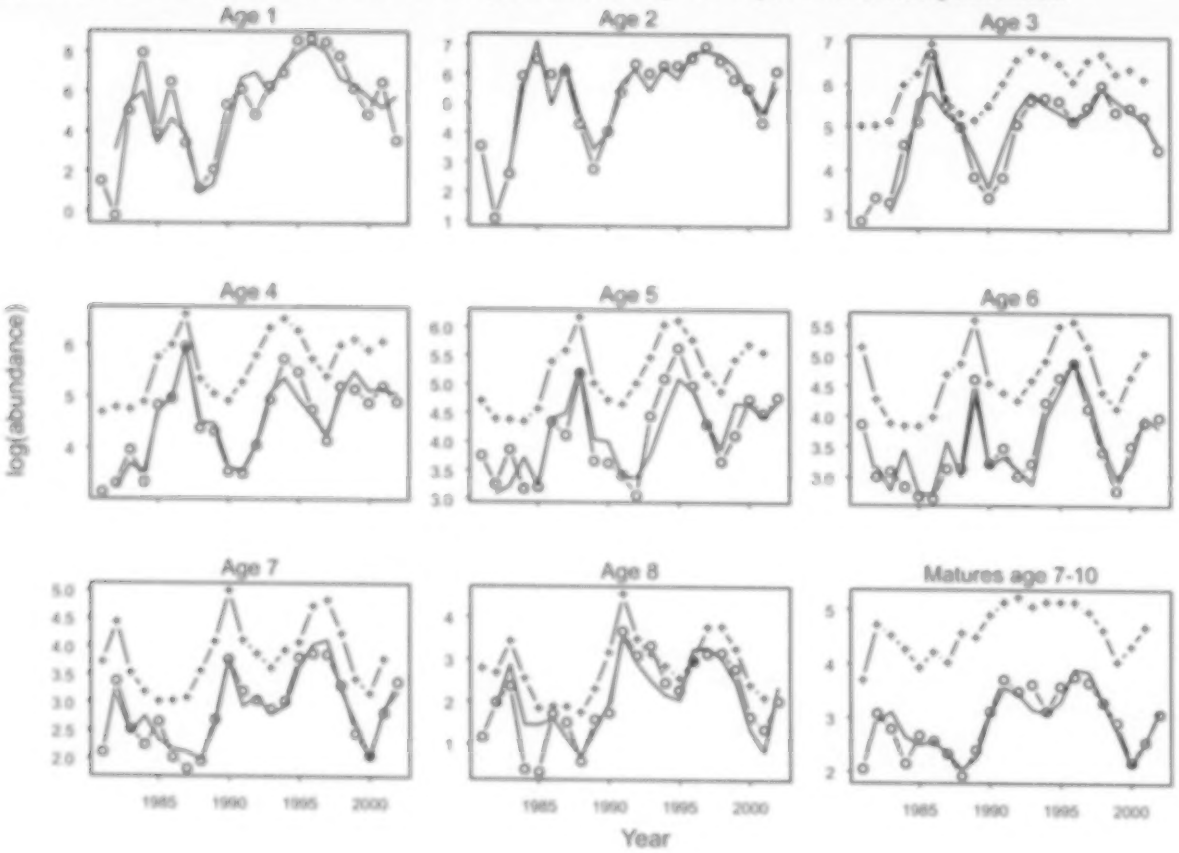
Fig. 2. Estimated values of abundance (N, lines with ●), model predictions from the models in Table 2 (lines), and virtual population analysis (VPA) estimates of abundance (lines with +; only calculated from age 3 and up). All values are log-transformed.



$$(3)\qquad N_t^{\text{mature}} = \sum_{a=\delta_{\text{mat}}}^{\delta_{\text{max}}} F(L_t^a)N_t^a$$

where F is a logistic function of mean length (see previous section). The average length L_t^a of cod of age a in year t is modelled in a similar way as abundance, with the difference that abundance may potentially influence growth in length. Also, we did not analyse length for ages 9 and 10, as the length of these age classes is of little ecological importance (almost all fish are mature anyway) and these data lack confidence.

$$(4a)\qquad L_t^1 = d_1 + e_1\log(N_{t-1}^{\text{mature}}) + f_{1,1}X_{t-1}^1 + f_{1,2}X_{t-1}^2 + \ldots + \varepsilon_{L_t^1}$$

$$(4b)\qquad L_t^2 = d_2 + e_2\log(N_{t-1}^1) + f_{2,1}X_{t-1}^1 + f_{2,2}X_{t-1}^2 + \ldots + \varepsilon_{L_t^2}$$

$$\vdots$$

$$(4h)\qquad L_t^8 = d_8 + e_8\log(N_{t-1}^7) + f_{8,1}X_{t-1}^1 + f_{8,2}X_{t-1}^2 + \ldots + \varepsilon_{L_t^8}$$

Statistical analyses and simulation

The parameters in the components of the matrix model were estimated using ordinary linear regression for each of the eqs. 2*a*–2*j* and 4*a*–4*h* separately. The set of *X*s to include in the model was determined using Akaike's information criterion adjusted for small samples (AIC_C; Hurvich and Tsai 1989). The AIC_C consists of two terms: one that measures the model's fit to the data, and one that gives a "penalty" for the number of variables; the model(s) with lowest AIC_C is (are) expected to minimize the difference between the predictions of the candidate model and the "true" model (Burnham and Anderson 1998). When applying linear regression to time-series data, it is important to make sure that the assumption of independent errors is not broken. We therefore subjected the residuals of the analysis to an autocorrelation analysis to examine whether the residuals of year t and year $t + 1$ were independent. Note, however, that even if the abundances are autocorrelated in time, this does not necessarily require a time-series analysis; as long as the residuals are uncorrelated in time (i.e., that the explanatory variables pick up the autocorrelation), an ordinary regression is justified.

Also of interest is whether the errors from the various models tend to correlate. For instance, if the abundance at age 3 tends to be overestimated in the same years as the

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Table 2. The selected regression models with estimated parameters.

Eq.	Selected model	SEs (excluding intercept)	σ	R^2
2a	$\log(N_t^1) = -5.03 + 7.52\log(N_{t-1}^{mat}) - 1.02\log(N_{t-1}^{mat})^2 + 1.25\text{Mesh}_t - 2.86\text{Harvest}_{t-1}^{5-10}$	2.79, 0.43, 0.76, 1.23	1.49	0.7
2b[a]	$\log(N_t^2) = 2.81 + (1 - 0.46)\log(N_{t-1}^1) - 0.75\text{Mesh}_{t-1}$	0.05, 0.27	0.47	0.87
2c[a]	$\log(N_t^3) = 2.87 + (1 - 0.46)\log(N_{t-1}^2) - 0.31\text{CodCap}_{t-1}$	0.06, 0.14	0.41	0.81
2d	$\log(N_t^4) = 1.51 + (1 - 0.15)\log(N_{t-1}^3) - 0.45\text{CodCap}_{t-1}$	0.06, 0.08	0.22	0.92
2e	$\log(N_t^5) = 0.66 + (1 - 0.23)\log(N_{t-1}^4)$	0.10	0.38	0.75
2f	$\log(N_t^6) = 0.78 + (1 - 0.21)\log(N_{t-1}^5) - 0.55\text{Harvest}_{t-1}^{5-10}$	0.08, 0.18	0.27	0.86
2g	$\log(N_t^7) = 0.91 + (1 - 0.24)\log(N_{t-1}^6) - 0.69\text{Harvest}_{t-1}^{5-10}$	0.08, 0.16	0.22	0.9
2h	$\log(N_t^8) = -0.42 + (1 + 0.40)\log(N_{t-1}^7) - 0.65\text{Harvest}_{t-1}^{5-10} - 0.15\log(N_{t-1}^4)$	0.24, 0.43, 0.07	0.51	0.76
2i	$\log(N_t^9) = 2.86 + (1 + 0.25)\log(N_{t-1}^8) - 2.18\text{Harvest}_{t-1}^{5-10} - 1.30\text{CodCap}_{t-1}$	0.24, 0.73, 0.34	0.97	0.84
2j	$\log(N_t^{10}) = 1.68 + (1 - 0.39)\log(N_{t-1}^9) - 1.85\text{Harvest}_{t-1}^{5-10}$	0.10, 0.63	0.8	0.85
4a	$\log(L_t^1) = 15.75 + 0.99\log(N_{t-1}^{mat}) + 0.21\text{NAO}_{t-1}$	0.28, 0.12	1.12	0.44
4b	$\log(L_t^2) = 17.32 + 0.40L_{t-1}^1 - 0.86\log(N_{t-1}^1) + 1.13\text{Temp}_{t-1}$	0.45, 0.29, 1.14	2.2	0.67
4c	$\log(L_t^3) = 1.89 + 1.26L_{t-1}^2 + 0.49\log(N_{t-1}^2) + 0.42\text{NAO}_{t-1}$	0.12, 0.27, 0.16	1.46	0.91
4d	$\log(L_t^4) = 0.77 + 0.77L_{t-1}^3 - 0.87\log(N_{t-1}^3) + 0.71\text{Temp}_{t-1}$	0.11, 0.48, 0.89	1.44	0.9
4e	$\log(L_t^5) = 30.81 + 0.64L_{t-1}^4 - 2.24\text{CodCap}_{t-1}$	0.12, 0.67	1.86	0.83
4f	$\log(L_t^6) = 39.00 + 0.57L_{t-1}^5 - 2.68\text{CodCap}_{t-1}$	0.12, 0.70	2.21	0.74
4g	$\log(L_t^7) = 27.73 + 0.76L_{t-1}^6 - 1.42\text{CodCap}_{t-1}$	0.10, 0.57	1.86	0.79
4h	$\log(L_t^8) = 19.43 + 0.89L_{t-1}^7 - 1.04\text{CodCap}_{t-1}$	0.16, 0.86	2.84	0.60

Note: The standard errors (SEs) for each parameter except the intercept (a) is given in the second column (given in the same order as in column 1). The third column shows the standard deviation (σ) of the error terms ($\varepsilon_{N,t} \sim \varepsilon_{N,t}$, $\varepsilon_{L,t} \sim \varepsilon_{L,t}$), and the last column shows the fraction of variance explained (R^2).

[a]One year (t = 1982) was an outlier, probably because the sampling methodology was somewhat different in the 1st year of the survey. This was therefore omitted from the analysis.

abundance at age 4, then this may indicate that both age groups are influenced by some variable that is not included in the model. Alternatively, both models may contain the same variable, but the relationship between this variable and the abundance is either not real or not correctly modelled.

Finally, we used the selected models to simulate the cod dynamics in 1982–1999, using the abundances N and the average length L of each age class in the first year as initial conditions. This procedure is fundamentally different from a simple fit to the data, as the observed cod data from the second year onwards are not used. First, N and L values for year 2 are predicted from the observed N and L values for year 1. Then, the predicted N and L values for year 2 are used to predict N and L for year 3, etc. The observed values of external variables (temperature, North Atlantic Oscillation (NAO), capelin abundance, and fishing mortality) are used throughout the simulation. The fish were assumed to die after the age of 10 (this simplification has very little consequence because of the very small number of cod in these age groups). For each time step in the simulation, we added the same random noise. The observed residual variance in each model component (ε in eqs. 1 and 3) is a combination of dynamic noise (process error, i.e., variance due to unexplained variation in real survival–reproduction) and observation error (measurement error, i.e., differences between real and estimated survival–reproduction) (Azerefegne et al. 2001). The proportion of each type, however, is unknown. For survival and reproduction, we assumed that each type contributes 50% of the observed residual variance. For growth in length, we assumed that all observed noise was dynamic (average length is generally easier to estimate than abundance). Observation noise only affects the prediction of a single year; in contrast, dynamic noise is carried on to subsequent years of the simulation.

Results

From the data on maturation and length between 1981 and 2002, we estimated the parameters of the equation $F(L) = e^{(\alpha+\beta L)}/[1+ e^{(\alpha+\beta L)}]$ to be $\alpha = -9.48$ (standard error (SE) = 1.74) and $\beta = 0.1316$ (SE = 0.0249). For ages 9 and 10, the length data were inaccurate and we assumed the proportion of matures to be 0.96 and 1.00, respectively, equal to the observed median proportion for these age groups. The survey estimates were lower than the VPA estimates, but closely correlated with the VPA (correlation; $r > 0.81$ for ages 3–8; Fig. 2). This was also the case for ages 7 and 8, which were estimated on the basis of survey data from the Barents Sea, as well as the fraction of matures.

We found that $A_{min} = 7$ and $A_{max} = 10$ gave the best fit to the data when model *3a* was fitted to the number of matures (eq. 3). In the selection of the models, the one with the lowest AIC_C value was chosen in all cases except one: for N^8, the model with the lowest AIC_C contained a term for both trend (Year) and $\text{Harvest}_{t-1}^{5-10}$, whereas the second best contained neither of the two. We decided to leave out Year_{t-1} but keep $\text{Harvest}_{t-1}^{5-10}$, as this was consistent with the models for N^7 and N^9 and as the difference in AIC_C value was only 1.49 (differences smaller than 2 are not regarded as significant; Burnham and Anderson 1998). The model showed a good fit to the data (Table 2; Fig. 2). The model indicated a strong negative effect of the cod–capelin ratio on the abundance of

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Fig. 3. Partial autocorrelation of the residuals of models 1*a*–1*j*. The dotted lines denote significant autocorrelation.

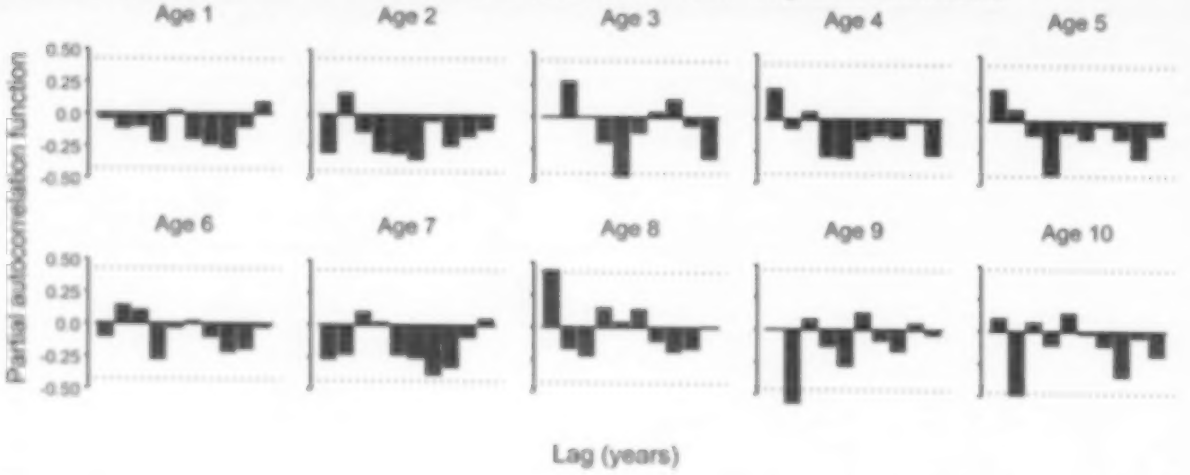
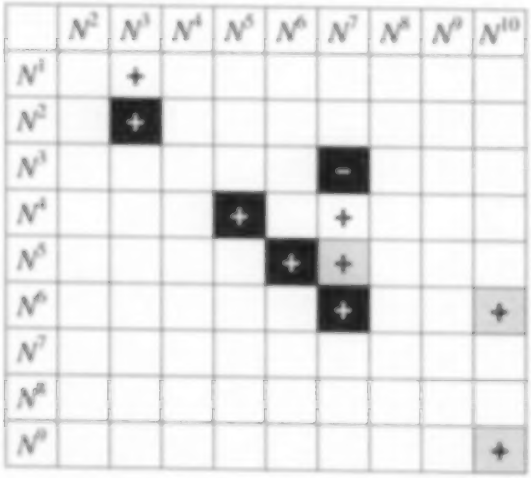


Fig. 4. Correlation patterns among residuals of models 1*a*–1*j*. The signs indicate whether correlations were positive or negative (only shown for $P < 0.1$), and the significance levels are indicated (solid, $P < 0.01$; shaded, $0.01 < P < 0.05$; open, $0.05 < P < 0.1$).



small fish (Table 2). This ratio also affected the growth of cod from ages 4–5 and up. For younger cod, growth depended on temperature or NAO (which are strongly correlated). We found no effect of capelin abundance or climate (sea temperature or NAO) on reproduction. We found effects of the overall harvest level on the survival of ages 4–5 and up; this variable was consistently better than the age-specific harvest. For 1-year-old cod (eq. 2*a*), there was evidence for a nonlinear effect of the abundance of matures (fitted using a quadratic term of N_{t-1}^{mat}; Table 2). There was no clear indication of nonlinearity for any other terms in the models.

An autocorrelation analysis of the residuals indicated that the model errors separated by 1 year were independent, with the exception of the model for 8-year-old cod (Fig. 3). For younger cod, there were some negative correlations at a 4- to 5-year lag. Overall, the results indicated that the age-8 model should be treated with some caution as the standard errors are underestimated, whereas an ordinary regression (as opposed to time-series analysis) is warranted for the other models. The residuals of the models tended to be correlated between age 1 and age 2 (i.e., in the years that the model overestimated, or underestimated, age 1, age 2 tended to be overestimated, or underestimated, as well). The same was true for ages 4, 5, and 6; a visual inspection indicates that there are two intercorrelated groups of variables (Fig. 4). This indicates that two uncorrelated factors, which have not been included in our models, influence the survival of these groups in concert. Such a pattern can also develop if the catchabilities of several age groups fluctuates in concert, but in that case, we would expect the extracted factors to be negatively autocorrelated in time, which they are not.

When the model is run using the observed time series of external variables (climate, prey abundance, and fishing mortality), the mean of the simulations (Fig. 5*a*) fit quite well to the observations, at least for around 12 years (until 1983–1984). It is perhaps most interesting that the model is able to explain the low abundance of matures in the late 1980s. Assuming that we know each year's actual per-capita reproductive rate (Fig. 5*b*) naturally yields better predictions for young cod but, in fact, increases the prediction errors for mature cod. The predictions for mature cod are substantially improved only if we know the actual survival rate of large (ages 4–6) immature cod (Fig. 5*d*). Thus, for this time series, our ability to understand the fluctuations of mature cod in the 1980s to 1990s appears mainly limited by our inability to predict the survival rate of large immature cod.

Discussion

The regression models generally showed a good fit to the data, considering that the models are fairly simple with only few parameters. Also, the variables included are largely consistent between models. Thus, we feel we can trust that there is a true effect of these factors.

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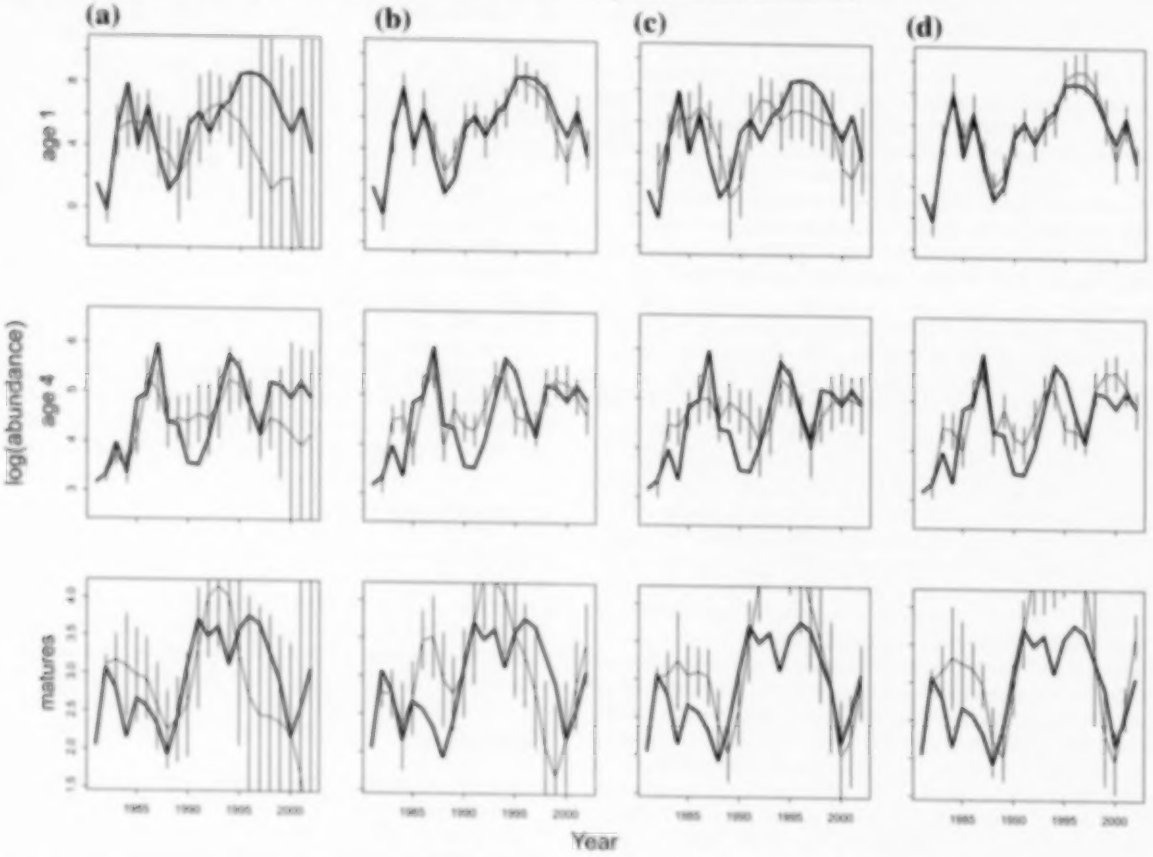
Fig. 5. Observed (thick line) and simulated abundance N (thin lines with error bars) of cod (*Gadus morhua*) between 1981 and 2002, showing the model's ability to recreate cod dynamics. Each column illustrates results of a simulation model run 100 times, each time initialized in 1982 (1981 was omitted because its values for young cod were unreliable; cf. footnote in Table 2). Error bars indicate 1 standard deviation. (*a*) Results of a simulation using the model as given in Table 2, with only initial abundance given. Whereas model predictions for the 2nd year depend on the observed abundance and body length for each age class in the 1st year, model predictions from the 3rd year onwards depend on the model predictions for the previous year, as well as observed values of external variables (temperature, NAO, capelin abundance, and fishing mortality). (*b*) As (*a*) except that we assume to know per capita reproduction for each year, so $\log(N^1)$ is set to equal the predicted $\log(N^{\text{mod}}_t)$ plus the observed values of $\log(N^1_t) - \log(N^{\text{mod}}_{t-1})$. (*c*) We assume to know the survival rate $\log(N^{\text{age}}_t) - \log(N^{\text{age}-1}_{t-1})$ from age 3 to age 6 (i.e., large immature cod). The values of $\log(N^{\text{age}}_t)$ (age = 4, 5, and 6) was set equal to the predicted $\log(N^{\text{age}-1}_{t-1})$ plus the observed values of $\log(N^{\text{age}}_t) - \log(N^{\text{age}-1}_{t-1})$. (*d*) The knowledge from (*b*) and (*c*) is combined using the procedures described in (*b*) and (*c*) to show both reproduction and survival rate.



The findings support previous studies on NEA cod. First, it is expected that harvesting negatively affects survival of cod from age 5 up, as well as reproduction (i.e., harvesting on mature fish before they spawn). The overall harvesting intensity (Harvest^{5-10}) was consistently a better predictor than the measures of age-specific fishing (i.e., the survival from ages 5 to 6 was affected more by the landing–abundance ratio for cod of ages 5–10 than by the landing–abundance ratio for 5-year-old cod). This is probably caused by larger uncertainty in the age-specific landing–abundance ratios.

Secondly, we found that the survival from ages 2 to 4 is negatively affected by the cod–capelin ratio, which is most likely caused by cannibalism from older cod in periods when there was a lack of capelin as a source of food, as shown by cod-stomach data (Ushakov and Prozorkevich 2002). This study confirms that increased cannibalism affects survival, as assumed by recent VPA analyses (ICES 2002*a*). The cod–capelin ratio also has a negative effect on growth from age 4 to age 8 (i.e., the growth during the last part of the immature stage and the first part of the mature stage, as also shown by Nilssen et al. (1994)). Both these effects of cod–capelin interactions are highly relevant for the cod's dynamics, meaning that during periods of low capelin abundance, fewer recruits will survive to the age of maturation, and maturation will be postponed. The fact that cod–capelin ratio consistently was a better predictor than just capelin abundance indicates that there is some effect of density-dependence.

The growth of the young cod was found to depend on both abundance and climate (although the role of the NAO versus the sea temperature is unclear). The effect of abundance on growth in length is not necessarily caused by com-

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petition (Myers and Cadigan 1993); rather, density and growth in length may both be affected by the same factor. Of special relevance is the mechanism discussed by Ottersen et al. (2002) with regard to length: a strong inflow of Atlantic water into the Barents Sea tends to lead to (*i*) high recruitment of 0-group fish (Sætersdal and Loeng 1987; Ellertsen et al. 1989; Ottersen et al. 1994) and (*ii*) distribution of the 0-group fish over a large area including the cold water masses in the eastern Barents Sea. Thus, an abundant year class is partly distributed in cold areas during the first 2–3 years of its life (when their movement capacity is limited). This helps to explain the negative relationship between abundance and length growth (Ottersen et al. 2002).

We found a negative correlation between 8-year-old cod and reproduction, measured using 1-year-olds in the following year (N_1^1). However, we view this result with some scepticism as we found no such correlation for other age groups. The same can be said for the negative correlation between abundance of 9-year-olds and the cod–capelin ratio.

The potentially interesting b coefficients (eq. 2), which in part reflect density-dependence, are significantly larger than zero for ages 1 to 7. These coefficients are difficult to interpret unless one has some information about whether catchability is correlated with abundance and how the correlation changes with the age. Godø et al. (1999) found no relationship between catchability and density for cod larger than 50 cm (age ≥4–5). Thus, the positive b coefficients for ages 6 and 7 may be interpreted as potential density-dependent survival. For 30- to 50-cm cod (around ages 3–4), Godø et al. (1999) found that catchability and density were positively correlated. However, the magnitude of the effect was quite modest (a 35% increase in catchability when density increased fivefold) compared with the large b coefficients at ages 2 and 3. Thus, cod survival may be significantly density-dependent for younger age classes, as also found by Myers and Cadigan (1993).

We expected to find a positive effect of temperature or NAO (which are positively correlated) on reproduction, as indicated by numerous studies (Ottersen et al. 2001; Ottersen and Stenseth 2001; Stenseth et al. 2002 and references therein). Likewise, we also expected reproduction to be correlated with capelin or the cod–capelin ratio, as capelin abundance is positively related to the amount of lipids stored in the cod liver (Marshall et al. 1999; Yaragina and Marshall 2000), which in turn has a positive effect on recruitment (Marshall et al. 2000). The lack of these effects may be caused by uncertainty (observation noise) in the estimates of age 1.

As a somewhat more critical test of the models (compared with just fitting), we started with simulations using data from 1982 and let the models "run free" thereafter. Although the results for each age class deviated considerably from the data, the simulation was able to mimic the spawning stock's decline in the end of the 1980, the increase until the early 1990s, and another decline in the 1990s. However, the variation between individual simulation results was extremely large for the second half of the 1990s. If we fed the model correct "reproduction" values (here, $\log(N_1^1) - \log(N_{-1}^{mat})$), the predictions for young cod improved, but the predictions for mature cod, in fact, resulted in the opposite. However, if we fed the model correct values for the "survival" of large immatures, the predictions for mature cod improved. This may indicate that our understanding of the fluctuations in the cod stock is hampered by a lack of knowledge about factors influencing survival of the large immatures. Therefore, marine science should perhaps put more focus on the survival of the immatures.

Altogether, we have shown that the a priori factors thought to be important for the variation in the abundance and natural mortality of NEA cod, in fact, can be tracked as signals in the estimates from the scientific survey. There is still great uncertainty about the absolute level of the population abundance and the natural mortality M, as seen by the discrepancy between the VPA estimates and the survey estimates. However, the estimates are closely correlated, and the reason that VPA estimates are larger may be that the natural mortality rate applied by the Arctic Fisheries Working Group is too low. We believe that models such as this one can contribute to an improved understanding of the population biology of the Barents Sea cod and that similar models may be useful with regard to other stocks and species of marine fish. As in NEA cod, we expect that such models must incorporate effects of a range of environmental and biotic factors, operating on different stages of the life cycle (Rothschild 2000). Such analyses may be an important step towards clarifying the interplay between intraspecific processes (leading to density-dependent relationship), interspecific processes (such as predator–prey relationships, also leading to density-dependent structures, direct or delayed), and climate (being a typical density-independent factor).

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Survival of Puget Sound chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*)

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Abstract: We tested for competition between pink salmon (*Oncorhynchus gorbuscha*) and chinook salmon (*Oncorhynchus tshawytscha*) originating from rivers in the Puget Sound area using coded-wire-tagged subyearling hatchery chinook salmon. Following a 2-year life cycle, many juvenile pink salmon enter Puget Sound in even-numbered years, whereas few migrate during odd-numbered years. During 1984–1997, juvenile chinook salmon released during even-numbered years experienced 59% lower survival than those released during odd-numbered years, a trend consistent among 13 chinook salmon stocks. Lower even-numbered-year survival of chinook salmon was associated with reduced first-year growth and survival and delayed maturation. In contrast, chinook salmon released into coastal streams, where few pink salmon occur, did not exhibit an alternating-year pattern of survival, suggesting that the interaction occurred within Puget Sound and the lower Strait of Georgia. Unexpectedly, the survival pattern of Puget Sound chinook salmon was reversed prior to the 1982–1983 El Niño: chinook salmon survival was higher when they migrated with juvenile pink salmon during 1972–1983. We hypothesize that chinook salmon survival changed as a result of a shift from predation- to competition-based mortality in response to recent declines in predator and prey abundances and increases in pink salmon abundance. Alternating-year mortality accounted for most of the 50% decline in marine survival of chinook salmon between 1972–1983 and 1984–1997.

Résumé : Nous avons évalué la compétition entre les saumons quinnat (*Oncorhynchus tshawytscha*) et les saumons roses (*Oncorhynchus gorbuscha*) provenant des rivières de la région du Puget Sound en utilizant des saumons quinnat de pisciculture âgés de moins d'un an et marqués avec des fils de fer codés. Après 2 ans de leur cycle, de nombreux jeunes saumons roses se déplacent vers le Puget Sound les années paires, mais peu le font les années impaires. En 1984–1997, les jeunes saumons quinnat relâchés durant les années paires ont connu une survie de 59 % inférieure à ceux qui ont été relâchés les années impaires et la tendance s'est maintenue dans 13 stocks de saumons quinnat. La survie réduite les années paires est associée avec une diminution de la croissance et de la survie la première année et une maturation retardée. En revanche, les saumons quinnat relâchés dans les cours d'eau côtiers, où il y a peu de saumons roses, n'ont pas expérimenté cette alternance d'une année à l'autre dans la survie, ce qui laisse croire que l'interaction se produit dans le Puget Sound ou le détroit de Géorgie inférieur. De façon inattendue, le pattern de survie des saumons quinnat de Puget Sound a été inversé avant l'El Niño de 1982–1983, alors que leur survie était plus élevée lorsqu'ils migraient en compagnie des saumons roses en 1972–1983. Notre hypothèse veut que la survie des saumons quinnat ait changé d'un contrôle de la mortalité par la prédation à un contrôle par la compétition en réaction au déclin récent des abondances de prédateurs et de proies et l'augmentation de l'abondance des saumons roses. La mortalité à tous les deux ans explique la plus grande partie du déclin de la survie en mer des saumons quinnat entre les périodes 1972–1983 et 1984–1997.

[Traduit par la Rédaction]

Introduction

Competition is recognized as an important factor affecting growth of Pacific salmon (*Oncorhynchus* spp.) in marine waters. Density-dependent growth has been observed among salmon during early marine life (Peterman 1984) and homeward migration (Rogers and Ruggerone 1993). Salmon originating from different regions or continents may intermingle in the North Pacific Ocean and compete for prey, leading to a reduction in growth (McKinnell 1995; Ruggerone et al. 2003). Competition for resources may also occur between species of salmon. For example, competition with pink

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salmon (*O. gorbuscha*) has led to reduced growth of sockeye salmon (*O. nerka*) (Bugaev et al. 2001; Ruggerone et al. 2003), coho salmon (*O. kisutch*) (Ogura et al. 1991), and chinook salmon (*O. tshawytscha*) (Grachev 1967), and has altered the diet (Tadokoro et al. 1996) and distribution of chum salmon (*O. keta*) on the high seas (Azumaya and Ishida 2000).

Few studies have demonstrated the effect of competition at sea on survival of salmon, although reduced growth is believed to lead to greater predation risk (Parker 1971) and to greater mortality during winter (Nasagawa 2000; Beamish and Mahnken 2001). Ruggerone et al. (2003) documented reduced growth and reduced smolt-to-adult survival of Bristol Bay sockeye salmon that co-inhabit offshore waters with abundant Asian pink salmon in odd-numbered years. In Puget Sound and British Columbia, competition between pink salmon and chum salmon was believed to reduce survival of chum salmon (Gallagher 1979; Beacham 1993; Fresh 1997). Furthermore, the unique abundance-at-age of adult Puget Sound chum salmon, which alternates between even- and odd-numbered years and therefore minimizes interactions with abundant juvenile pink salmon in even-numbered years, was believed to be an evolutionary response to competition during early marine life (Smoker 1984; Salo 1991). Recently, Levin et al. (2001) suggested that competition with hatchery-produced chinook salmon may lead to reduced survival of native Snake River spring/summer-run chinook salmon during years of low ocean productivity.

Pink salmon, which are the most abundant Pacific salmon and the youngest at maturation, often appear to be the dominant salmonid involved in competitive interspecies interactions. Pink salmon tend to feed at a lower trophic level than other salmonids at sea and to have the least direct diet overlap with chinook salmon, which tend to feed at a higher trophic level (Welch and Parsons 1993). Few studies have examined competition between pink salmon and chinook salmon, the largest and oldest anadromous salmonid at maturation. However, Grachev (1967) reported that scale growth of Kamchatka chinook salmon during the first 2 years at sea was inversely related to pink salmon abundance, suggesting that these two species may compete for prey, either directly or indirectly through the food web.

In Puget Sound, Washington, nearly all juvenile pink salmon migrate to sea during even-numbered years and return to spawn during the following odd-numbered year. The invariable 2-year life cycle of pink salmon and the distinct odd-year adult-return pattern provide a unique opportunity to evaluate competition by comparing release-to-recovery survival rates of subyearling chinook salmon during odd- versus even-numbered years. We hypothesized that survival of chinook salmon would be lower among fish entering Puget Sound during even-numbered years, i.e., years when juvenile pink salmon are abundant. Competition for prey might be relatively great within Puget Sound and the lower Strait of Georgia, where chinook and pink salmon densities are relatively high. We also examined potential competition effects on length at age and age composition of chinook salmon. A reduction in length or a shift to older fish at maturation during years of high pink salmon abundance would be consistent with the competition hypothesis, since reduced growth at sea tends to lead to older ages at maturation in salmon (Helle 1979; Rogers 1987; Healey 1991). Additionally, we were interested in determining whether competitive interactions have increased in recent years in response to climatic and oceanographic changes and the apparent reduction of prey in the Strait of Georgia and Puget Sound region (Beamish et al. 2000, 2001). It is especially important to identify and quantify factors affecting Puget Sound chinook salmon, since naturally produced chinook salmon and some hatchery stocks are listed as threatened species under the US Endangered Species Act (National Marine Fisheries Service 1999).

Methods

The competition hypothesis was tested by comparing release-to-recovery survival rates of subyearling chinook salmon originating from 10 Puget Sound hatcheries and 3 Fraser River / lower mainland British Columbia hatcheries. During even-numbered years, chinook salmon released from these hatcheries follow numerous juvenile pink salmon of primarily natural origin into marine waters, whereas in odd-numbered years almost no juvenile pink salmon are present. Both species rear in Puget Sound and the Strait of Georgia before migrating primarily through the Strait of Juan de Fuca before entering the North Pacific Ocean. The distinct odd/even-year abundance pattern of Puget Sound and Fraser River pink salmon provided a natural experimental control to test the competition hypothesis. Furthermore, almost no pink salmon originate from coastal Washington and lower Vancouver Island, therefore chinook salmon releases from nine hatcheries in these areas were examined to evaluate whether stocks that rear largely outside Puget Sound and the Strait of Georgia were similarly influenced. If pink salmon influence the population characteristics of chinook salmon only within the confines of Puget Sound and the Strait of Georgia, we would expect to see an alternating pattern among chinook salmon from Puget Sound and the lower mainland but not among those from coastal Washington and lower Vancouver Island.

Survival of chinook salmon was estimated from the release and recovery of hatchery fish receiving implanted coded wire tags (CWTs). The CWT is a small wire (0.25 mm × 1 mm) containing a binary code that links the recovered salmon to the specific release location, release date, age at release, and other relevant information. Groups of more than 100 000 juvenile salmon can be injected with a tag containing an identifying code prior to release, but the percentage of hatchery-produced chinook salmon receiving a CWT is typically 6% or less. All fish receiving CWTs in this study were marked by removing the adipose fin so that fishery observers could readily detect CWT fish in the fisheries. Recovery of CWT fish in fisheries is achieved by initially identifying fish with a missing adipose fin, scanning the selected fish for the presence of a CWT using a magnetic field detector, then surgically removing it from the snout of the fish at the laboratory. At least 20% of the salmon catch in each commercial salmon fishery is examined for CWT fish (Johnson 1990). Sampling of sport fisheries may be somewhat less than 20% and most fish returning to the hatcheries are sampled for CWTs. Counts of CWT salmon recovered in fisheries or hatcheries are expanded by the agencies using

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the percentage of total fish sampled for CWTs in each fishery and time period. The CWT data are collected and checked by state, provincial, federal, and tribal agencies before delivery to the Pacific States Marine Fisheries Commission, where the data are validated for format consistency and stored (Johnson 1990).

The CWT release and recovery data were obtained from the Regional Mark Information System database, which is maintained by the Pacific States Marine Fisheries Commission (Pacific States Marine Fisheries Commission 2003). The database was first queried for tag codes representing groups of chinook salmon released into streams feeding into the study area. These tag codes were then used to query the database for daily recoveries of each tag code in each recovery location. The period of investigation began with releases in 1972 and ended with releases in 1997, since recoveries after this period were incomplete. Survival indices were based on the release of 53.5 million CWT chinook salmon from hatcheries within the study area (Table 1).

Several restrictions were applied in selecting CWT data in order to eliminate potential bias from unusual tag groups. The analysis was limited to chinook salmon released as subyearlings into fresh water during April through July. The analysis excluded tag groups having body weights exceeding 2 standard deviations above or below the mean. Returning hatchery-produced salmon recovered on stream spawning grounds were excluded from the analysis because sampling of streams for CWT fish was not consistent throughout the time period.

The survival rates reported here are indices of survival based on the recovery-to-release ratio for each tag code, where recoveries occurred across multiple years and among fish ranging from age 1 to age 6:

$$(1)\qquad \text{Survival index} = \sum_{age\ 1}^{age\ 6} (\text{recoveries})(\text{juvenile release})^{-1}$$

When a hatchery used more than one tag code in a release year, the survival rates were weighted by the number of fish released, then averaged. Some fish recovered in fisheries may not have been maturing in the year of capture, thus the survival rates reported here overestimate release-to-adult survival to the extent that immature fish were recovered that would have died. However, the survival indices underestimate survival of some stocks (all British Columbia stocks and Stillaguamish and Tulalip Bay stocks in Puget Sound) because hatcheries in these watersheds do not recover most returning adult salmon. Fisheries implementing catch and release may also cause underestimation of survival to recovery, since this mortality is largely unreported. The survival index largely reflects mortality in marine waters, but it also reflects some mortality in fresh water (Pacific Salmon Commission 2001).

Age of recovered fish was based on the difference between the recovery year and the parent spawning year; thus, fish spending one winter at sea were classified as age 2. Age-specific recovery rates, or partial survival rates, were calculated from age-specific recoveries and total fish released:

$$(2)\qquad \text{Age-specific recovery rate} = \sum_{age\ x}^{age\ y} (\text{recoveries})(\text{juvenile release})^{-1}$$

Age composition of returning salmon was calculated for the cohort of salmon released each year from each watershed. Since most chinook in the study area return to spawn at ages 3 and 4, the percentage of recovered fish older than 3 was used to test for a shift in age composition. Most CWT chinook salmon recovered at hatcheries are measured (fork length) by hatchery personnel. Hatchery data were used to compare age-specific lengths of fish released during odd- versus even-numbered years.

Virtual population analysis (VPA; Hilborn and Walters 1992; Coronado and Hilborn 1998) was used to reconstruct survival of odd- versus even-year-release cohorts at age 2 in an effort to identify mortality associated with delayed maturation. VPA provides an estimate of the number of chinook salmon surviving to a given age after the effects of delayed and early maturation are removed. The total number of salmon alive at age 2 (N^*), including those captured or escaped to hatcheries at ages other than 2, was calculated with the following equation:

$$(3)\qquad N^* = C_1 s_1 + C_2 + C_3/s_3 + C_4/s_3 s_4 + C_5/s_3 s_4 s_5 + C_6/s_3 s_4 s_5 s_6$$

where C_t is the number of fish of a given tag group recovered at age t, and s_t is the survival rate from age $t-1$ to age t. Age-specific natural mortality rates, which are assumed by VPA to be constant from year to year, were obtained from the Pacific Salmon Commission (2001). N^* was then substituted for recoveries in survival index (eq. 1).

The potential effect of pink salmon on chinook salmon was tested by comparing survival rates, lengths at age, and age composition depending on whether the juvenile chinook salmon were released during an odd- or even-numbered year. Survival rates and age-composition proportions were normalized using the arcsine transformation prior to statistical analysis, then retransformed when reported in the text. A two-factor Type I analysis of variance (ANOVA) was used to test for statistical differences in survival, length at age, and age composition. The two factors were year of chinook salmon release (odd- or even-numbered year) and stock. Multivariate time series analysis of these data was not possible because stock-specific data were not available for all years.

The analysis of differential survival rates of chinook salmon resulting from odd- versus even-numbered-year releases was based on the premise that pink salmon fisheries, whose season can overlap with the presence of chinook salmon, would not artificially create or mask the underlying pattern of survival. The presence of pink salmon fisheries may lead to longer fishing seasons and potentially greater harvest of CWT chinook salmon in odd-numbered years, leading to an alternating year pattern of recoveries and potential bias. To test for a potential fisheries-related bias, exploitation rates of chinook salmon released from Puget Sound hatcheries during odd- and even-numbered years were compared during recent and early time periods. During 1984–1997, chinook salmon released into the Stillaguamish

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Table 1. Number of years and average annual release of coded-wire-tagged (CWT) subyearling chinook salmon (*Oncorhynchus tshawytscha*) by stock and time period.

		1972–1983			1984–1997		
Stock	Subarea	No. of years	No. of CWT fish per year	Average weight (g)	No. of years	No. of CWT fish per year	Average weight (g)
Puget Sound							
Duwamish	Mid-Sound	10	170 029	4.2	12	246 780	5.9
Grover	Mid-Sound	0	0		13	171 134	7.7
Lake Washington	Mid-Sound	5	192 375	5.6	3	196 029	4.8
Minter	South Sound	0	0		10	206 778	8.3
Nisqually	South Sound	4	42 500	5.2	14	209 292	8.5
Nooksack	North Sound	9	77 120	5.2	9	288 285	5.6
Sammish	North Sound	4	173 139	4.1	12	202 742	5.0
Skagit	North Sound	2	105 342	3.4	6	197 942	6.4
Stillaguamish	Mid-Sound	0	0		10	112 653	5.6
Tulalip	Mid-Sound	0	0		5	180 524	5.0
Coastal Washington							
Quinault	Middle	8	87 612	11.4	11	182 865	10.5
Humptulips	Middle	0	0		6	190 255	6.4
Queets	Middle	6	64 269	10.7	13	148 892	12.0
Soues	North	0	0		10	183 579	6.1
Willapa	South	3	211 337	5.5	6	321 508	5.7
Lower British Columbia							
Chehalis	Lower Fraser R.	0	0		14	143 362	2.5
Chilliwack	Lower Fraser R.	2	104 877	6.1	14	124 233	6.4
Capilano	Lower Mainland	10	179 042	5.7	14	116 928	6.7
Chemainus	SE Vancouver I.	4	87 833	7.3	11	74 775	8.8
Cowichan	SE Vancouver I.	2	38 109	2.7	10	105 266	5.3
Qualicum	SE Vancouver I.	12	123 762	6.4	14	218 842	6.5
Robertson	SW Vancouver I.	10	162 722	5.0	14	261 806	5.9

River and Tulalip Bay were excluded from this analysis because the hatcheries did not attempt to recover fish. Exploitation rates for each stock were calculated as follows:

$$\text{(4)}\quad \text{Exploitation rate} = \sum_{age\,1}^{age\,6}(\text{fisheries recoveries})(\text{total recoveries})^{-1}$$

Trends in pink salmon abundance since the early 1970s were examined in relation to chinook salmon survival and abundance. Pink salmon harvest and spawning escapement data for Puget Sound, Fraser River, and southern Vancouver Island were obtained from the Washington Department of Fish and Wildlife (J. Packer, 600 Capitol Way North, Olympia, WA 98502, USA, personal communication), Fisheries and Oceans Canada (L. Hop Wo, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, personal communication), and the Pacific Salmon Commission (B. White, 600 – 1155 Robson Street, Vancouver, BC V6E 1B5, personal communication).

Results

Time-trend analysis

Analysis of release-to-recovery survival estimates during 1972–1997 revealed that the pattern of survival from odd- and even-numbered-year releases of subyearling Puget Sound chinook salmon switched in the early 1980s, corresponding to the 1982–1983 El Niño event. During release years 1984–1997, survival of even-numbered-year releases of chinook salmon was consistently lower than that of odd-numbered-year releases, whereas during 1972–1983, survival of even-numbered-year releases tended to be relatively high (Fig. 1). Survival during 1984–1997 tended to be lower than during 1972–1983, a pattern that was opposite to that of adult pink salmon abundance (see below). Within the early period, salmon survival was exceptionally high during 1974–1976, years that immediately preceded the shift in the Pacific Interdecadal Oscillation Index (Mantua et al. 1997). More years of CWT data and numbers of tagged fish released per year were available during 1984–1997 than during the earlier period (Table 1), therefore the statistical power of tests was greater for the recent period. Thus, subsequent analyses of survival, size at age, and age composition were analyzed by period of release: 1972–1983 and 1984–1997.

Fishery exploitation rates

Rates of exploitation of chinook salmon were examined to test for potential bias influenced by pink salmon fisheries, which occur in odd-numbered years. During release years 1984–1997 (two-factor ANOVA, $F_{[1,64]} = 0.879$, $P = 0.352$) and 1972–1983 ($F_{[1,533]} = 0.533$, $P = 0.475$), exploitation rates of chinook salmon did not differ by odd and even year of release, indicating that survival estimates were not biased

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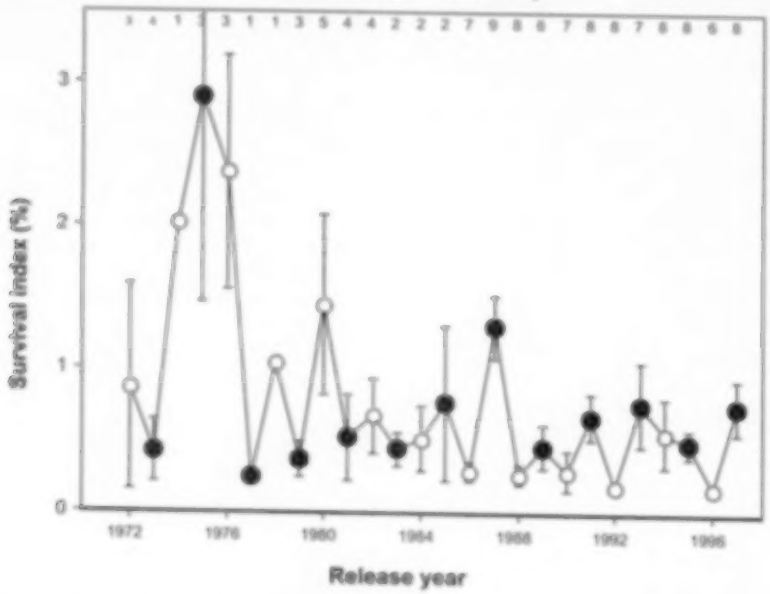
Fig. 1. Survival index for subyearling chinook salmon (*Oncorhynchus tshawytscha*) released into Puget Sound streams during 1972–1997. Survival values during even- (○) and odd-numbered (●) years are shown. Values are unweighted means (±1 standard error) of one or more stocks. The number of contributing stocks each year is shown at the top.



by the fisheries. This observation is further supported by the age-specific recovery-rate estimates described below. Exploitation rates were not influenced by potential interaction between odd/even year and stock during either period ($P > 0.50$).

Pink salmon abundance

Juvenile Puget Sound pink salmon migrate to sea during even-numbered years and return to spawn during odd-numbered years. Exceptionally few adult pink salmon return during even-numbered years, averaging less than 1% of odd-year abundances. Odd-numbered-year returns of adult pink salmon corresponding to juvenile migration years 1984–1996 averaged 1.34 million fish (±0.22 million fish (standard error, SE)) and were approximately 80% greater than returns corresponding to 1972–1982 juvenile migration (Fig. 2). Most pink salmon return to northern Puget Sound rivers such as the Skagit and Snohomish. Both run size ($F_{[1,11]} = 5.232$, $P = 0.043$) and spawning escapement ($F_{[1,11]} = 9.094$, $P = 0.012$) were significantly greater during 1984–1997 than in the earlier period. The corresponding production of pink salmon fry entering the relatively confined waters of Puget Sound was approximately 43 million per even-numbered year during 1984–1997 and 24 million during 1972–1983, assuming 3.1% survival at sea (International Pacific Salmon Fisheries Commission 1986; Heard 1991).

The Fraser River is a major producer of pink salmon and, like Puget Sound, primarily produces juvenile pink salmon that migrate to sea during even-numbered years and return to spawn during odd-numbered years. During smolt years 1984–1997, odd-numbered-year returns of Fraser River pink salmon averaged 14.7 million (±2.1 million (SE)) and were approximately 29% greater than returns during 1972–1983 (Fig. 2). Pink salmon spawning escapements averaged 192% more spawners during 1984–1997 than during the 1972–1983 smolt period ($F_{[1,11]} = 11.393$, $P = 0.006$), indicating significantly greater numbers of juvenile pink salmon during 1984–1997. Thus, approximately 470 million pink salmon fry per even-numbered year entered the lower Strait of Georgia during 1984–1997 compared with 367 million pink salmon fry per even-numbered year in 1972–1983, assuming 3.1% survival at sea.

In contrast to Puget Sound and the Fraser River, exceptionally few pink salmon return to streams along the Washington coast (Phinney and Bucknell 1975) and along the west coast of Vancouver Island (L. Hop Wo, Fisheries and Oceans Canada, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, personal communication). Southeast Vancouver Island produces small runs of pink salmon that return in approximately equal numbers during both odd- and even-numbered years (Fig. 2). Spawning-escapement estimates were four times larger during 1984–1997 (average 44 000) than during 1972–1983 (average 10 300), largely because of efforts to rebuild the runs.

Puget Sound chinook salmon

During release years 1984–1997, release-to-recovery survival of Puget Sound chinook salmon was significantly lower among fish released from hatcheries during even-numbered years than among those released during odd-numbered years (two-factor ANOVA (odd/even year, stock); $F_{[1,74]} = 25.548$, $P < 0.001$). This pattern was consistent among chinook salmon originating from all 10 drainages (Fig. 3) and there was no significant interaction between the effects of odd/even year and stock (ANOVA factor interaction; $F_{[9,74]} = 0.376$, $P = 0.94$). On average, juvenile chinook salmon released during

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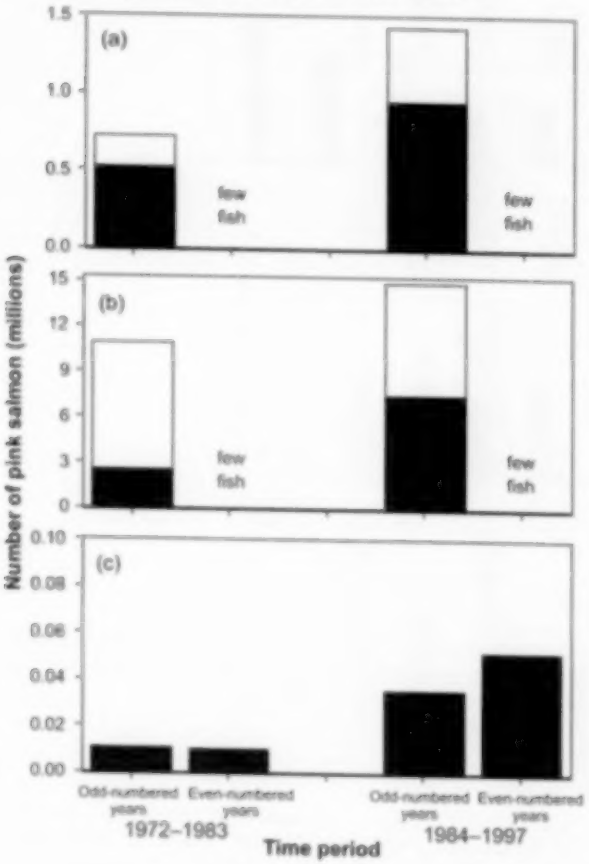
Fig. 2. Average spawning escapement (solid bars) and harvest (open bars) of pink salmon (*Oncorhynchus gorbuscha*) originating from (*a*) Puget Sound rivers, (*b*) the Fraser River, and (*c*) southeast Vancouver Island rivers during odd- and even-numbered years of return. Values correspond to juvenile migrations during 1972–1983 and 1984–1997. Few pink salmon return to the Washington coast and west Vancouver Island.



even-numbered years, corresponding to years of abundant juvenile pink salmon, experienced 62% lower survival than those released during odd-numbered years.

Puget Sound chinook salmon were recovered after spending from one (age-2 fish) to five (age 6) winters at sea. Recovery rates of age-2 ($F_{[1,74]} = 14.086$, $P < 0.001$), age-3 ($F_{[1,74]} = 23.763$, $P < 0.001$), age-4 ($F_{[1,74]} = 24.006$, $P < 0.001$), and age-5 ($F_{[1,74]} = 20.468$, $P < 0.001$) chinook salmon were significantly lower among fish released during even-numbered years than among those released during odd-numbered years. Few age-6 chinook salmon were recovered and they were not tested. Lower age-specific recovery rates of fish released during even-numbered years were observed among chinook originating from all 10 drainages (Fig. 4), and percent reductions were similar among the age groups, ranging from 56% among age-4 fish to 65% among age-3 fish. Of these age groups only age-2 chinook salmon did not interact with both odd- and even-year pink salmon. No interaction effect between odd/even-numbered year and stock was detected ($F_{[9,74]} < 1.05$, $P > 0.431$). The consistency in reduced recovery rates of age-2, -3, -4, and -5 chinook salmon released during even-numbered years indicates that the difference in survival occurred during the first year at sea.

During release years 1972–1983, release-to-recovery survival rates of Puget Sound chinook salmon did not differ significantly between even- and odd-numbered years ($F_{[1,22]} = 1.964$, $P = 0.175$). No significant difference in survival was detected among age-2 ($F_{[1,22]} = 2.413$, $P = 0.135$), age-3 ($F_{[1,22]} = 1.826$, $P = 0.183$), and older chinook salmon ($P > 0.28$) (Fig. 5). However, average survival rates during odd-numbered years tended to be lower among all six stocks for which data were available (Fig. 3), a pattern that was opposite to that during 1984–1997. The lack of a statistically significant difference in survival among odd- and even-numbered-year releases was largely due to the exceptionally high survival of chinook salmon released in 1975 (Fig. 1). Excluding 1975, chinook survival was significantly less during odd-numbered years ($F_{[1,19]} = 5.257$, $P = 0.033$). No interaction between odd/even-numbered year and stock was detected ($F_{[5,19]} = 0.127$, $P = 0.98$).

Mean release-to-recovery survival declined 50% from 1972–1983 (average 0.88% survival) to 1984–1997 (average 0.44% survival) (excluding Stillaguamish, Grover, Minter, and Tulalip stocks, which had few data during the early period). However, survival of odd-numbered-year releases was relatively constant across the two time periods (0.61% and 0.68%, respectively), whereas survival of even-numbered-year releases experienced an 82% decline from 1972–1983 to 1984–1997 (1.15% and 0.21%, respectively; Fig. 1; paired *t* test, df = 5, $t = -3.287$, $P = 0.028$). This suggests that the decline in survival of Puget Sound chinook salmon during the 25-year period of investigation was associated with releases of chinook salmon during even-numbered years, not releases during odd-numbered years.

Length at age of CWT chinook salmon recovered at Puget Sound hatcheries was examined to determine whether salmon released in even-numbered years experienced reduced growth compared with those released in odd-numbered years during the 1984–1997 release period. Age-2 chinook salmon released during even-numbered years (mean ± SE = 436 ± 7.9 mm) were significantly smaller than those released during odd-numbered years (453 ± 8.3 mm; Fig. 6; two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,43]} = 4.860$, $P = 0.033$). Age-3 chinook salmon released during even-numbered years (659 ± 8.5 mm) tended to be smaller than those released during odd-numbered years (672 ± 7.9 mm), even though these fish experienced growing seasons during both even- and odd-numbered years ($F_{[1,55]} = 3.862$, $P = 0.054$). Lengths of age-4 and age-5 chinook salmon were not significantly different when they were released as juveniles during even- versus odd-numbered years ($P > 0.32$). The odd/even-numbered-year growth pattern of age-2 and age-3 chinook salmon was consistent among stocks, as indicated by the insignificant ANOVA interaction values ($P > 0.05$). Too few data were available to evaluate length at age during 1972–1983. These data indicate that growth reduction occurred during the first year, and that growth and mortality

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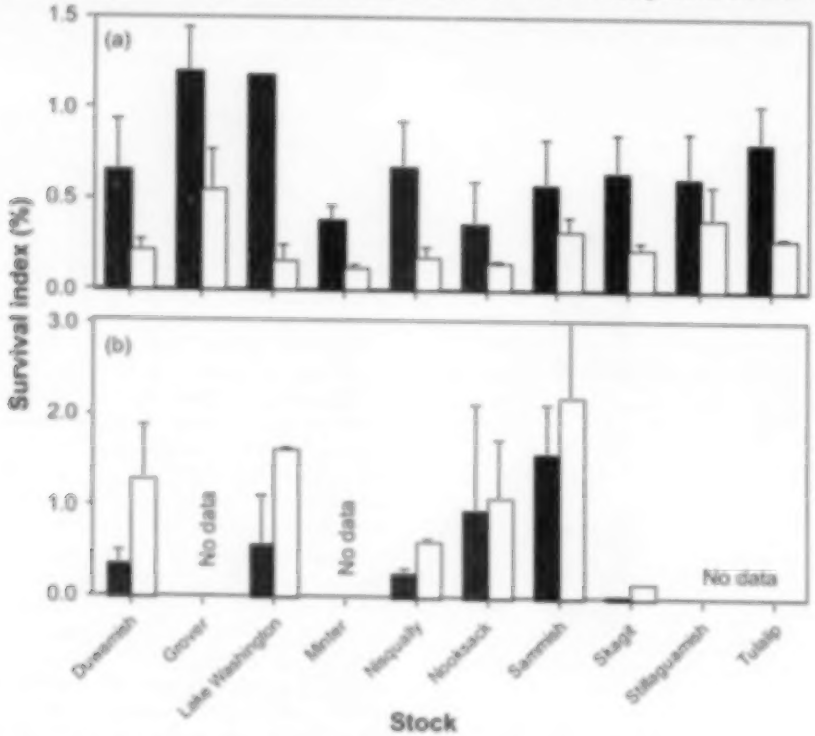
Fig. 3. Release-to-recovery survival of subyearling coded-wire-tagged (CWT) chinook salmon released into Puget Sound streams in odd- (■) and even-numbered (□) years during (*a*) 1984–1997 and (*b*) 1972–1983. Values are given as the mean + 1 standard error.



during subsequent years masked the differential growth during early marine life.

Age composition of recovered chinook salmon was examined to determine whether even-numbered-year releases led to an older age at maturation during 1984–1997, as might be expected if growth of these fish was reduced. Most Puget Sound chinook salmon mature at ages 3 and 4, thus the percentage of fish recovered at age 4 and older was used to test the hypothesis. The percentage of chinook salmon recovered at age 4 and older tended to be greater (12.3 ± 3.2%) among fish released during even-numbered years than during odd-numbered years (two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,74]} = 3.674$, $P = 0.059$). This pattern was consistent among 8 of the 10 stocks (Fig. 7); there was no significant interaction between the effects of odd/even year and stock ($F_{[1,74]} = 0.270$, $P = 0.980$). In contrast, age composition during 1972–1983, a period when pink salmon abundance was low, did not vary between odd- and even-numbered release years ($F_{[1,22]} = 0.101$, $P = 0.754$).

For the 1984–1997 period, VPA was used to estimate the proportion of chinook salmon mortality that was associated with delayed maturation as opposed to mortality during the first year at sea. Delayed maturation explained approximately 1% of the difference in mortality between odd- and even-numbered-year releases, indicating that most mortality associated with the alternating-year pattern occurred during the first year in marine waters. This finding is also apparent in Fig. 4, which shows that the survival pattern was established during the first year and was apparent among chinook salmon of all ages. Although delayed maturation was apparent among even-numbered-year releases of chinook salmon, its effect on overall survival was minor compared with that which occurred during the first year.

Chinook salmon in the lower mainland of British Columbia

Hundreds of millions of juvenile pink salmon emigrate from the Fraser River, British Columbia, during even-numbered years, but almost none emigrate during odd-numbered years. During 1984–1997, release-to-recovery survival of chinook salmon released into lower mainland streams (Chilliwack, Chehalis, and Capilano) during even-numbered years was 51% lower than that of those released during odd-numbered years (Fig. 8; two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,36]} = 5.547$, $P = 0.024$), a trend that was consistent with that in Puget Sound and among for each lower mainland stock (ANOVA factor interaction: $F_{[2,36]} = 0.224$, $P = 0.80$). The combined average reduction of even-numbered-year migrants in Puget Sound and the lower mainland streams was 59%. Age-specific recovery rates of lower mainland stocks tended to be lower among age-2 ($F_{[1,36]} = 3.812$, $P = 0.059$), age-3 ($F_{[1,36]} = 5.522$, $P = 0.024$), age-4 ($F_{[1,36]} = 3.139$, $P = 0.085$), and age-5 ($F_{[1,36]} = 2.997$, $P = 0.0920$) chinook salmon that were released during even-numbered years, but most relationships were not statistically significant ($\alpha = 0.05$), owing to small sample sizes and the low power of the test. Too few data were available to evaluate changes in length.

The percentage of chinook salmon recovered at age 4 and older (release years 1984–1997) was markedly greater among

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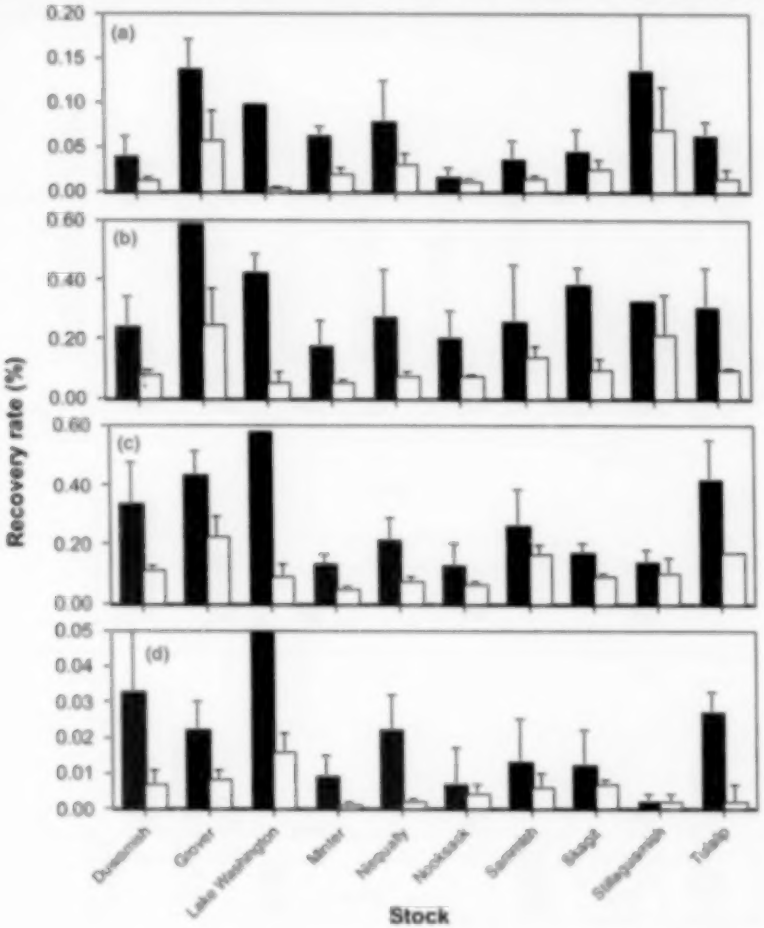
Fig. 4. Recovery rates of (*a*) age-2, (*b*) age-3, (*c*) age-4, and (*d*) age-5 subyearling chinook salmon released into Puget Sound streams in odd- (■) and even-numbered (□) years during 1984–1997. Values are given as the mean + 1 standard error.



those released during even-numbered years ($F_{[1,35]} = 4.914$, $P = 0.048$), a trend that is consistent with that of Puget Sound chinook salmon and for each lower mainland stock (ANOVA factor interaction: $F_{[2,35]} = 0.023$, $P = 0.977$). Greater age at maturity of lower mainland British Columbia chinook salmon during even-numbered years was associated with lower survival and large numbers of juvenile pink salmon.

During 1972–1983, few data were available to test for odd/even-numbered-year survival of lower mainland chinook salmon, and no odd/even-numbered-year pattern was detected (Fig. 8; $F_{[1,9]} = 1.472$, $P = 0.256$).

Washington coast chinook salmon

Essentially no pink salmon are produced by streams along the Washington coast and streams to the south, therefore juvenile chinook salmon originating from these streams would not encounter pink salmon during early marine life. During 1984–1997, release-to-recovery survival of chinook salmon released into coastal Washington streams (Willapa, Humptulips, Quinault, Queets, Sooes) did not differ between odd- and even-numbered-year releases (Fig. 9; two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,20]} = 0.925$, $P = 0.344$). Recovery rates of age-2, -3, -4, and -5 chinook salmon also did not differ between odd- and even-numbered-year releases ($F_{[1,80]} < 1.15$, $P > 0.30$). No interaction effect between odd/even-numbered year and stock was detected ($F_{[4,80]} = 0.381$, $P = 0.82$).

Fewer data were available to test for the odd/even-numbered-year effect on survival of Washington coast stocks during 1972–1983. Release-to-recovery survival of chinook salmon released into coastal Washington streams did not differ between odd- and even-numbered-year releases (Fig. 9; two factor ANOVA (odd/even-numbered year, stock); $F_{[1,10]} = 0.006$, $P = 0.939$), but the power of this ANOVA was weak (0.062).

Lower Vancouver Island chinook salmon

In contrast to survival of chinook salmon released into streams on the lower mainland of British Columbia, release to recovery survival of chinook salmon released into lower Vancouver Island streams (Qualicum, Chemainus, Cowichan, and Robertson) did not differ among odd- and even-numbered-year releases ($F_{[1,40]} = 0.185$, $P = 0.670$). Few

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Fig. 5. Recovery rates of (*a*) age-2, (*b*) age-3, (*c*) age-4, and (*d*) age-5 subyearling chinook salmon released into Puget Sound streams in odd- (■) and even-numbered (□) years during 1972–1983. Values are given as the mean + 1 standard error.

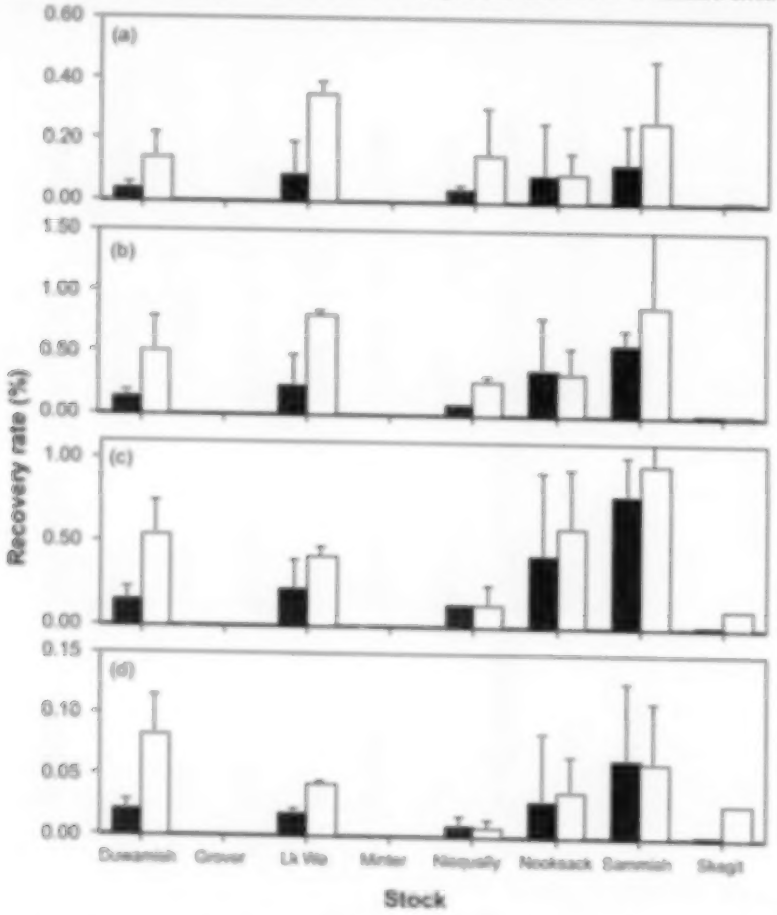
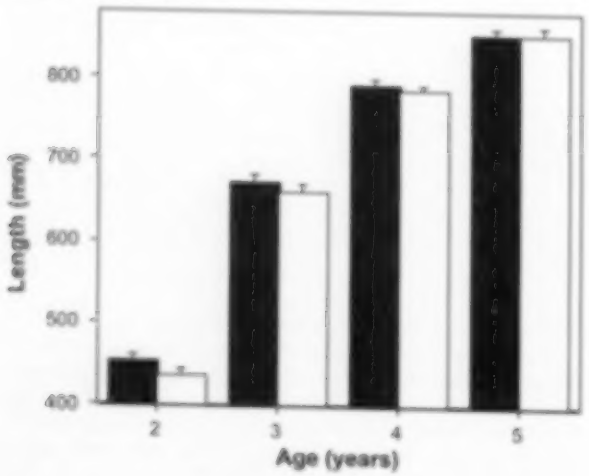


Fig. 6. Mean length at age of chinook salmon recovered at eight Puget Sound hatcheries after release in odd- (■) and even-numbered (□) years during 1984–1997. Values are given as the mean + 1 standard error.



pink salmon originate from lower Vancouver Island, and the small runs returning to southeast Vancouver Island are nearly equal during odd- and even-numbered years.

Discussion

The key finding of this study was that survival rates of subyearling chinook salmon in Puget Sound and the lower mainland of British Columbia alternated between even- and odd-numbered years during the 25-year period of investigation. During 1984–1997, survival of chinook salmon was significantly less during even- versus odd-numbered years, whereas during 1972–1983, survival tended to be greater during even-numbered years. The transition in salmon survival rate corresponded to the 1982–1983 El Niño event, one of the largest on record (Wolter and Timlin 1998). Below we provide evidence that this major El Niño and subsequent and relatively frequent El Niño events (Wolter and Timlin 1998) contributed to the observed pattern of chinook salmon survival by influencing a shift from predation-based to competition-based mortality. We hypothesize that chinook salmon tended to experience greater survival in even-numbered years during 1972–1983 because prey availability

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Fig. 7. Percentages of age-4 and older Puget Sound chinook salmon recovered from releases of CWT subyearling chinook salmon in odd- (■) and even-numbered (□) years during 1984–1997. Values are given as the mean + 1 standard error.

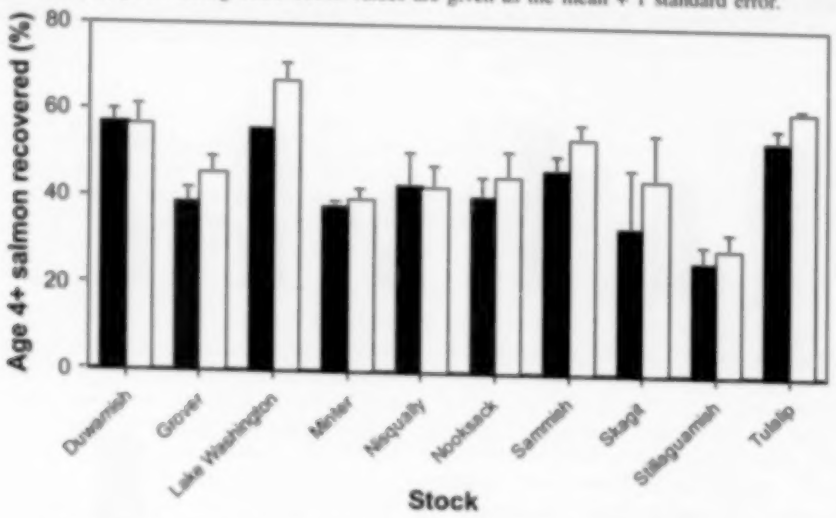
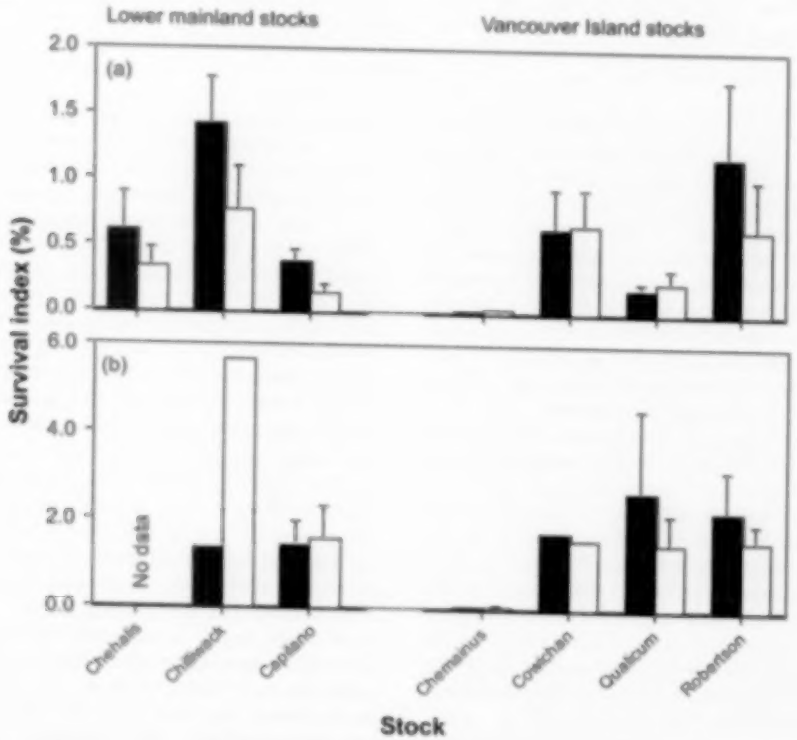


Fig. 8. Release-to-recovery survival of subyearling CWT chinook salmon released into streams in lower mainland British Columbia and lower Vancouver Island in odd- (■) and even-numbered (□) years during (*a*) 1984–1997 and (*b*) 1972–1983. Values are given as the mean + 1 standard error.



was relatively great and pink salmon provided a buffer against predation. After the 1982–1983 El Niño, low survival of chinook salmon during even-numbered years was related to increased competition with juvenile pink salmon in Puget Sound and the Strait of Georgia. Competition was great during this period because pink salmon abundance was high and oceanographic conditions had led to low annual prey availability. Size-selective predation likely contributed to chinook salmon mortality through competition and reduced growth.

During 1984–1997, chinook salmon released into Puget Sound streams during even-numbered years experienced reduced growth and survival during the first year at sea and a

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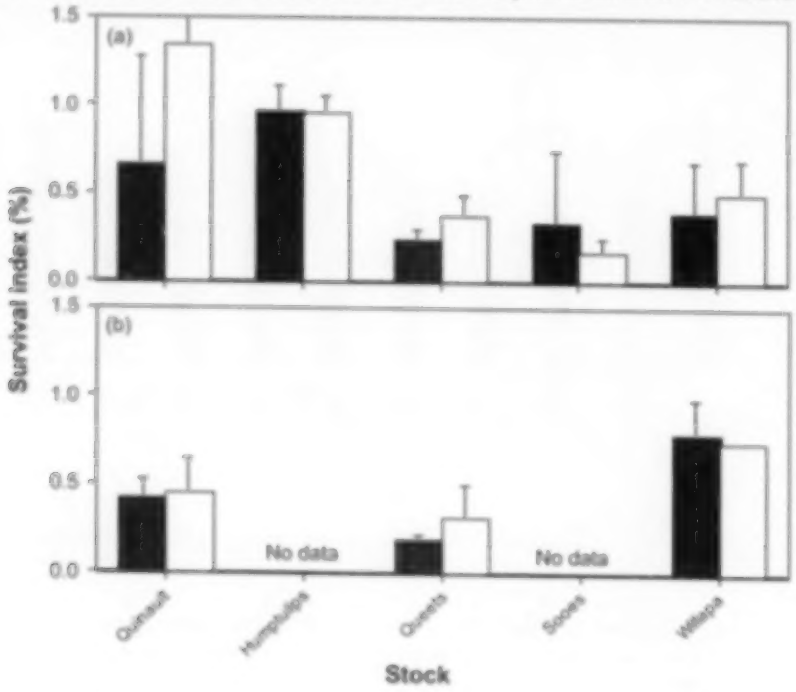
Fig. 9. Release-to-recovery survival of subyearling CWT chinook salmon released into coastal Washington streams in odd- (■) and even-numbered (□) years during (*a*) 1984–1997 and (*b*) 1972–1983. Values are given as the mean + 1 standard error.



delay in age at maturation. These even-numbered-year migrant chinook salmon entered Puget Sound with the progeny of odd-numbered-year adult pink salmon, which were exceptionally abundant compared with even-numbered-year adult pink salmon. The pattern of lower survival and delayed maturation of even-numbered-year migrants was also observed among chinook salmon released into lower mainland British Columbia streams; these chinook salmon follow the highly abundant Fraser River pink salmon into the Strait of Georgia. In contrast, no alternating-year survival pattern was detected among chinook salmon released into streams along the Washington coast and lower Vancouver Island, where pink salmon abundance was exceptionally low. These observations indicate that the pattern of chinook salmon survival was established while they were rearing in Puget Sound and the Strait of Georgia. Since relatively few pink salmon are found in southern Puget Sound, it is likely that the interaction occurred after chinook migrated into northern Puget Sound. Findings of reduced growth and delayed maturation of chinook salmon provide further support for the competition hypothesis. The magnitude of the interaction was large (an average of 59% reduction in survival among 13 stocks) and explains a significant portion of the decline in chinook salmon survival during 1972–1997.

In contrast to recent studies showing competition between pink salmon and sockeye or chum salmon (Ruggerone et al. 2003), in this study the mechanism of competition between juvenile pink and chinook salmon is not obvious because it apparently involves indirect rather than direct interactions between the species. Pink salmon (30–34 mm in length) rapidly migrate through estuaries, and most enter Puget Sound and the Strait of Georgia in April, although some fry continue entering marine waters in late May (Heard 1991). Pink salmon fry typically follow marine shorelines for several weeks, then move to epipelagic waters in May (Healey 1980). After rearing in marine waters for nearly 3 months, most juvenile pink salmon leave the lower Strait of Georgia and Puget Sound in July at a length of approximately 100 mm (Healey 1980). However, many still occupy the Strait of Juan de Fuca during August and some remain in inshore waters through fall (Hartt and Dell 1986). After leaving inside waters, most juvenile pink salmon migrate northward, primarily within a 40 km wide band along the coast.

The hatchery-produced subyearling chinook salmon tested here were primarily released into streams during May and June at approximately 6.3 ± 1.41 g (86 ± 5 mm), a somewhat similar size to many pink salmon during May and June because pink salmon had reared in marine waters for approximately 1.5 months. Most hatchery-produced subyearling chinook salmon likely migrate rapidly downstream to marine waters. Like pink salmon, subyearling chinook salmon rear in shallow nearshore waters for days or weeks before dispersing to epipelagic areas (Healey 1991). Most chinook salmon remain inside Puget Sound and the Strait of Georgia until October and November before entering the North Pacific Ocean (Healey 1982). Further, some chinook salmon overwinter in inshore waters. Thus, the period of potential overlap between the two species in Puget Sound and the Strait of Georgia is from approximately May through July. Some naturally produced chinook salmon may leave estuaries and enter nearshore marine waters as early as March and April (Healey 1980) and may therefore have greater overlap

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with pink salmon. Hence, large numbers of pink salmon enter marine waters first and may influence prey composition prior to the arrival of most naturally produced and hatchery-produced chinook salmon.

We hypothesize that during 1984–1997, pink salmon primarily influenced prey availability for chinook salmon through food-web dynamics rather than by direct competition for the same prey. Both pink and chinook salmon are opportunistic and generalized consumers of both pelagic and epibenthic prey and will consume similar prey when foraging together (Healey 1980). However, pink salmon typically consume lower trophic level prey (small invertebrates) during early spring and summer, whereas juvenile chinook salmon tend to prefer larger invertebrates and small fishes (Healey 1980; Fresh et al. 1981; Welch and Parsons 1993). Healey (1980) noted that pink salmon in the Strait of Georgia may reduce zooplankton abundance. Likewise, Shiomoto et al. (1997) reported that pink salmon in the central North Pacific Ocean can reduce prey availability for salmon, leading to reduced growth and survival (Ruggerone et al. 2003). Juvenile pink salmon enter Puget Sound prior to most chinook salmon and their impact on lower trophic level prey might reduce growth and survival of larger zooplankton species and small fishes and larvae that are consumed by chinook salmon. Unfortunately, food-web dynamics in this region are poorly understood and the dependence of higher trophic level species on lower trophic level prey has not been quantified (Harrison et al. 1983; Bornhold 1999). We do know that peak zooplankton production in Puget Sound and the Strait of Georgia occurs in April or May and that zooplankton abundance and body size decrease thereafter (Bornhold 1999). Thus, many juvenile chinook salmon enter marine waters during a period of declining availability of invertebrate prey, which may enhance the potential for inter- and intra-specific competition.

The switch in the alternating-year survival pattern of chinook salmon corresponded to the 1982–1983 El Niño. Pearcy (1992) noted that the 1982–1983 El Niño had a significant effect on oceanographic conditions and caused a shift in distribution of many marine fishes in the Pacific Northwest. The 1982–1983 El Niño and subsequent more frequent El Niño events were associated with higher sea-surface temperatures in Puget Sound (Bornhold 1999). Although continuous records are not available, abundances of many species in Puget Sound were markedly different before and after the event and may have influenced the switch in the survival pattern of chinook salmon.

Salmon predator populations appeared to be markedly greater during the 1970s than during the 1990s. For example, abundances of piscivorous birds declined more than 50% from the late 1970s to the 1990s (Puget Sound Water Quality Action Team 2002). Dogfish (*Squalus acanthias*), an important predator on juvenile salmon (Beamish et al. 1992), were also relatively abundant during the 1970s and early 1980s (Ketchen 1986), but their status was considered depressed during the 1990s (Puget Sound Water Quality Action Team 2002). Beamish and Neville (1995) estimated that river lamprey (*Lampetra ayresi*) consumed many chinook salmon in the Fraser River plume during the early 1990s, but in Puget Sound this species is listed as a federal and state species of concern (Washington Department of Fish and Wildlife 2004), suggesting that its abundance may be relatively low. Hake (*Merluccius productus*) reportedly can consume numerous juvenile salmon (Beamish and Neville 2001); their abundance in Puget Sound declined 97% from the early 1980s to the late 1990s (Puget Sound Water Quality Action Team 2002). Of the key predators on salmon, only harbor seals (*Phoca vitulina richardsi*), which typically consume adult salmon (Zamon 2001), have increased in abundance during the recent period (Puget Sound Water Quality Action Team 2002). These observations support our hypothesis that predation on juvenile Puget Sound salmon was likely greater during the 1970s. Our observation that survival of chinook salmon tended to be greater when they migrated with numerous pink salmon during 1972–1983 was unexpected, and the most likely explanation involves predation. Consumption of numerous pink salmon by subyearling chinook salmon is unlikely because the species are similar in size at this life stage. We propose that pink salmon provided a buffer to predation on juvenile chinook salmon, leading to greater survival of chinook salmon entering Puget Sound during even-numbered years from 1972 to 1983.

Significant changes in prey species have also occurred since the late 1970s. Bornhold (1999) reported that the timing of peak zooplankton abundance in the Strait of Georgia shifted from May during the 1960s and 1970s to April in the 1990s (no data for the 1980s), apparently in response to higher temperatures. This shift in zooplankton timing may have benefited juvenile pink salmon, which enter marine waters early (April) and were much more abundant during 1984–1997. In contrast, the spawning biomass of Cherry Point herring (*Clupea pallasii*), a spring-spawning stock that was once the largest in Puget Sound, was 60% lower during 1984–1997 than during 1973–1983 (Stout et al. 2001; $F_{[1,25]} = 43.929$, $P < 0.001$), a trend that may have been influenced by the shift in zooplankton timing. Progeny of these late-spawning herring may be important prey of juvenile chinook salmon. Although the spawning biomass of Cherry Point herring has exhibited a gradual decline since the first survey in 1973, it declined sharply in the early 1980s, a trend that corresponds to the switch in juvenile chinook salmon survival and the increase in pink salmon abundance. Potentially, pink salmon may influence growth and survival of larval and small juvenile herring, since the two species consume similar prey, such as copepods (Simenstad et al. 1979; Fresh et al. 1981). In contrast, most early-spawning stocks of herring in Puget Sound have not significantly declined and those in the Strait of Georgia are relatively abundant. Beamish et al. (2001) suggested that herring may compete with coho salmon for prey, especially during the recent period, when prey production appeared to be relatively low. Another source of juvenile chinook salmon prey are groundfish larvae, but most populations in Puget Sound are considered depressed (Puget Sound Water Quality Action Team 2002). Intraspecific competition among hatchery-produced chinook salmon may have contributed to lower prey availability during 1984–1997 because annual numbers of juvenile chinook salmon released into Puget Sound increased from 45 ± 3 million during 1972–1983 to 53 ± 7 million during 1984–1997 (G.T. Ruggerone, unpublished data). Numbers of chinook salmon released during odd- and even-numbered years in each period were nearly identical. We

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propose that the shift in peak zooplankton timing, reduced zooplankton abundance, decline in abundances of Cherry Point herring and other larval fishes, and greater abundance of pink salmon have contributed to increased competition between chinook and pink salmon during 1984–1997.

Few data are available to evaluate the growth of juvenile chinook salmon rearing in Puget Sound during the study period. Beamish et al. (2000, 2001) suggested that growth of juvenile coho salmon in the Strait of Georgia might have been low in the 1990s compared with the 1970s in response to shifts in climate, reduced prey availability, and increased competition. Growth of Puget Sound pink and coho salmon after one winter spent at sea was markedly greater before than after the 1982–1983 El Niño event (G.T. Ruggerone, unpublished data). Our analysis indicated that growth of juvenile chinook salmon during their first year at sea was significantly less when they were competing with pink salmon during 1984–1997, but too few CWT data were available to examine age-specific growth rates during 1972–1983. These observations indicate that salmon may have grown less while rearing in Puget Sound during 1984–1997, which suggests lower prey availability and a greater potential for competition.

Our observations suggest that predation-related mortality was relatively great during the 1970s, whereas prey availability and competition may have been more important to survival of chinook salmon in the 1980s and 1990s. This hypothesis is consistent with the "critical size and period hypothesis" proposed by Beamish and Mahnken (2001), which states that predation during early marine life and growth-related mortality late in the first marine year are key to determining year-class strength of salmon. In the Strait of Georgia, the recent decline in survival of coho salmon appeared to be primarily related to lower prey production associated with a climate shift and greater influence of competition for prey (Beamish and McFarlane 1999). However, lower coho salmon survival was associated with climate and ocean changes in 1989 (Beamish et al. 2000; Welch et al. 2000) rather than the 1982–1983 El Niño, which corresponded to the shift in the alternating-year pattern of chinook salmon survival. Both coho and chinook salmon appeared to be influenced by reduced prey availability during the recent period, but they responded differently to specific climate events. This variation may reflect differences in smolt size, timing of migration, habitat and prey preferences, and interactions with predator species.

The findings of this study involved hatchery-produced chinook salmon but have implications for naturally produced chinook salmon in Puget Sound protected by the US Endangered Species Act. Most naturally produced subyearling chinook salmon are somewhat smaller and more variable in size (~60–90 mm) when they enter Puget Sound than hatchery-produced chinook salmon (80–100 mm). This study indicated that reduced growth was associated with reduced survival. Smaller chinook salmon are likely more vulnerable to effects of reduced prey caused by competition. Thus, competition-related mortality in marine waters is linked to conditions in freshwater and estuarine habitats to the extent that these habitats contribute to the size of chinook salmon entering Puget Sound.

While the dynamics of trophic interactions connecting pink salmon to the alternating-year pattern of Puget Sound chinook salmon survival remain unknown, data show that chinook salmon growth and survival were significantly reduced among even-numbered-year migrants during 1984–1997. These data suggest that prey availability in Puget Sound and the Strait of Georgia was not sufficient to support existing numbers of juvenile chinook salmon in the presence of numerous pink salmon without inducing higher mortality rates. Competition is likely most important during periods when climate and oceanographic conditions limit prey production, such as during 1984–1997. Additional research is needed to evaluate the complex trophic dynamics that we infer from the unique alternating-year survival pattern of Puget Sound chinook salmon.

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Estimating reference fishing mortality rates from noisy spawner–recruit data

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Abstract: We review and evaluate methods of estimating reference fishing mortality rates from spawner–recruit (SR) data to obtain maximum sustainable yield. Using Monte Carlo simulations, we found that a reference fishing mortality rate derived from the maximum likelihood estimates of the SR parameters was less biased than reference fishing mortality rates obtained using the mode of the marginal probability distribution for the maximum rate that spawners produce recruits or by finding the fishing mortality rate that maximizes the expected yield. However, the maximum likelihood method produced the most variable estimates, at times leading to substantial under- or over-exploitation of the population. In contrast, the decision theoretic method of maximizing the expected yield exhibited less variability, produced higher yields, and substantially reduced the risk of overexploiting the population. We show how these methods can be extended to include information from other populations. Bayesian priors for the SR parameters, obtained through meta-analyses of population dynamics at some higher organizational level (e.g., the species), may be used to assess the plausibility of parameter estimates obtained for a single population or combined with the data for the population of interest. Reference fishing mortality rates are then estimated from the resulting joint posterior distribution.

Résumé : Nous examinons et évaluons les méthodes pour estimer les taux de référence de la mortalité due à la pêche à partir des données de reproducteurs–recrues (SR) afin d'obtenir le rendement maximal soutenable. L'utilisation de simulations de Monte Carlo indiquent qu'un taux de référence de la mortalité due à la pêche dérivé d'estimations de vraisemblance maximale des paramètres SR comporte moins d'erreur qu'un taux obtenu en utilisant le mode de la distribution de la probabilité marginale du taux de production maximale de recrues par les reproducteurs ou alors en trouvant le taux de mortalité due à la pêche qui maximise le rendement attendu. Cependant, la méthode de vraisemblance maximale produit les estimations les plus variables, ce qui quelquefois mène à d'importantes surexploitations ou sous-exploitations de la population. En revanche, la méthode basée sur la théorie de décision qui maximise le rendement attendu produit moins de variabilité, donne des rendements plus élevés et réduit de façon importante le risque de surexploiter la population. Nous montrons que ces méthodes peuvent être étendues de manière à inclure de l'information provenant d'autres populations. Les distributions bayésiennes a priori des variables SR, obtenues par méta-analyse de la dynamique de population à un niveau d'organisation supérieur (e.g., l'espèce), peuvent servir à évaluer la vraisemblance des estimations des variables obtenues pour une seule population ou combinées avec des données de la population en question. Les taux de référence de mortalité due à la pêche sont ensuite estimés à partir de la distribution jointe a posteriori obtenue.

[Traduit par la Rédaction]

Introduction

Biological reference points are indices based on the biological characteristics of a fish stock and the characteristics of its fishery. They are used to gauge whether specific management objectives are being achieved, provide the link between stock assessment and management objectives (Caddy and Mahon 1995), and provide a basis for risk analysis of management actions (Punt and Hilborn 1997). As the use of biological reference points becomes more prevalent in fisheries management, assessment of the precision of biological reference point estimates and development of methods that incorporate uncertainty into biological reference point estimation become more crucial (Caddy and McGarvey 1996; Richards and Maguire 1998; Overholtz 1999).

The most important source of uncertainty in estimating the long-term productivity of a fishery is the degree of density dependence in the spawner–recruit (SR) relationship (Getz et al. 1987; Myers et al. 1999). However, many SR data sets contain only limited information about SR parameters for the population of interest (Myers et al. 1999). When estimated using only data from an individual population, SR

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parameter estimates are at times biologically implausible (e.g., estimates of the maximum rate at which spawners produce recruits that are infinite) or are poorly determined (Barrowman and Myers 2000; Gibson and Myers 2003*a*), particularly when there is little contrast in the SR data. Despite this uncertainty, the maximum likelihood estimates (MLE) of the SR parameters are sometimes taken to be the best estimates and used to calculate the fishing mortality rate that produces maximum sustainable yield (F_{msy}).

Several methods have been proposed to deal with uncertainty in the SR relationship, including alternative reference points that do not explicitly include an SR component, methods that do not require specification of the functional form of the SR model, and methods that explicitly include uncertainty in the SR parameter estimates or model choice. For example, the reference fishing mortality rate $F_{x\%}$ is the fishing mortality rate that reduces the spawning biomass per recruit (SPR) to x% of its unfished level (Goodyear 1977; Shepherd 1982). This reference point is based on the premise of protecting spawning biomass but does not require an SR relationship for its estimation. However, the selection of an appropriate value for x is problematic and may be obtained only with reference to the productivity of the population (or other populations) or based on experience (Mace and Sissenwine 1993; Mace 1994; Clark 2002). Similarly, reference points based on yield per recruit (YPR) analyses (Beverton and Holt 1957) may also require adjustment based on stock productivity. An example is the adoption of $F_{0.1}$ (Gulland and Boerema 1973) when experience with F_{max} suggested that it advocated fishing mortality rates that exceeded the rates that would produce MSY.

Bayesian and decision theoretic methods have been used to explicitly include parameter uncertainty in the reference point estimation framework. Clark (1991) suggested that a production-based reference F could be estimated without knowledge of the true SR model by finding the fishing mortality rate that maximizes the minimum yield (F_{mmy}) over two SR models and a range of model parameters. Ianelli and Heifetz (1995) integrated over the likelihood surface for two SR parameters to obtain the marginal probability density for the slope at the origin of the SR relationship. Ianelli and Heifetz (1995) do not directly calculate a reference F from the marginal probability density for the slope at the origin, although their method does directly incorporate uncertainty in this parameter into their risk assessment. Chen and Holtby (2002) used the marginal probability density for the SR slope at the origin to estimate the probability density for F_{msy}. This approach has the advantage that uncertainty in the half-saturation constant is explicitly included and that the marginal probability density for α can be used to assess the precision of the resulting reference F. Its disadvantage is that all possible values of the SR parameters are considered equally favourable. If some points in the SR parameter space produce equilibrium yields at MSY that are higher than at other points, these points may be considered more favourable. A decision theoretic approach to estimating a reference point combines the probability for the model parameters with management objective criteria such as maximizing yield (Frederick and Peterman 1995). Brodziak (2002) used a decision theoretic approach to estimate a reference F that maximizes the expectation of the yield over two SR models (the Ricker and Beverton–Holt) and three values of a shape parameter for each model. This reference point, $F_{max[E]Y}$, includes uncertainty in the SR parameters and uncertainty in model selection as well as the consequences of adopting a reference F in its estimation.

A major problem with reference point estimation based on SR analyses is that the long SR time series spanning a range of stock sizes required for the analyses are simply unavailable for many populations (Caddy and Mahon 1995). Drawing upon the idea that populations of the same species (or closely related species) share similar life history strategies, meta-analytic methods have been developed that allow SR parameter estimates from several populations to be combined (Myers and Mertz 1998; Myers et al. 1999, 2001). These analyses provide probability distributions for the SR parameters at some higher organizational level (e.g., the species) and may be used as priors for Bayesian analyses (Hilborn and Walters 1992; Carlin and Louis 1996) of population dynamics for stocks where little or no data exist about the stock under investigation. When these priors are combined with data for the population of interest, the resulting joint posterior distribution for the population-specific SR parameters include information about the population under investigation as well as information obtained from similar populations. The posterior distribution can then be used to estimate a reference F using either its mode (analogous to the MLE of F_{msy} from single-species data) or the marginal distribution for the slope at the origin or by finding the fishing mortality rate that maximizes the expectation of the catch over the posterior distribution for the SR parameters.

In summary, fisheries biologists have several options for estimating a reference F depending on the available data (Table 1). In the absence of sufficient data for a production model, the researcher may choose to use an alternative reference point (e.g., $F_{x\%}$) or may use a decision theoretic approach by assuming that all parameter values within some bounds are equally plausible. When the researcher has sufficient population-specific data for a production model, other options are available. The researcher may calculate F_{msy} using either the MLE of the SR parameters or the mode of the marginal probability distribution for slope at the origin (we will refer to this reference point as F_{msy_0} to distinguish it from the MLE-based estimate of F_{msy}). Alternatively, the researcher may use a decision theoretic approach such as finding the fishing mortality rate that maximizes the expectation of the yield based on the likelihood surface for the SR parameters. If the researcher does not have population-specific SR data but has priors for the SR parameters obtained from other populations, reference F values may be found in similar ways. The researcher may estimate a reference F using either the mode of the joint prior distribution for the SR parameters or the mode of the marginal probability distribution for the maximum rate that spawners produce recruits or by finding the fishing mortality rate that maximizes the expectation of the yield. Finally, when both population-specific data and data from other populations are available, the joint posterior distributions for the SR parameters may be obtained and used to estimate reference F values. In the following sections, we apply these methods and address the question of which is best for estimating a reference F.

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Table 1. Summary of methods for estimating reference fishing mortality rates.

Data requirements	Maximum likelihood and alternatives	Marginal probability density for α	Decision theoretic methods
Insufficient data for a production model	Alternatives: $F_{\max}$, $F_{x\%}$, $F_{0.1}$		$F_{\min}$
Population-specific data only	$F_{\min}$ from the MLE of α and R_0	Integration of the likelihood over R_0 ($F_{\max}$)	$F_{\max E[\gamma]}$ (likelihood only)
Data from other populations only	$F_{\min}$ from the mode of the prior for α and R_0	Integration of the prior for α and R_0 over R_0 ($F_{\max}$)	$F_{\max E[\gamma]}$ (priors only)
Combined data	$F_{\min}$ from the mode of the posterior for α and R_0	Integration of the posterior for α and R_0 over R_0 ($F_{\max}$)	$F_{\max E[\gamma]}$ (priors and likelihood)

Note: Methods are presented in the context of the Beverton–Holt SR model, parameterized in terms the slope of the model at the origin of the SR model (α) and the asymptotic recruitment level (R_0). The maximum likelihood methods (MLE) use the mode of the SR likelihood or probability surface as the estimate of α that is used to estimate $F_{\min}$. The marginal (marg) probability density for α is found by integrating over R_0 and the optimal F is estimated using the mode of the resulting distribution. The decision theoretic method finds the value of F that maximizes the expectation of the catch over α and R_0. msy, maximum sustainable yield; mmy, maximized minimum yield.

Estimating reference fishing mortality rates using population-specific data

In this section, we compare three methods of estimating reference F values when only population-specific data are available. We use data from two anadromous alewife (*Alosa pseudoharengus*) populations as examples: the Gaspereau River, Nova Scotia, and Miramichi River, New Brunswick. Both populations are exploited commercially as they ascend their natal rivers to spawn. Descriptions of the fisheries and data collection are provided by Chaput and Atkinson (2001) and Gibson and Myers (2001). Gibson and Myers (2003*b*) provide details of the assessment modeling used to estimate the SR time series, maturity rates, and natural mortality rates.

For estimating $F_{\max E}$ and $F_{\max E[\gamma]}$, we will need to place bounds on the range of plausible SR parameter values. We make use of a meta-analysis of the population dynamics of eight alewife populations using mixed effects models (Gibson and Myers 2003*b*). One purpose of this analysis was to derive probability distributions for the logarithm of the maximum lifetime reproductive rate (Myers et al. 1999) and the logarithm of the carrying capacity per unit area for alewife at the species level, assuming normal distributions for these parameters. The resulting random effects distribution for the log of the maximum lifetime reproductive rate has a mean of 3.06 and a standard deviation of 0.1. The random effects distribution for the log of the carrying capacity has a mean of 4.01 and a standard deviation of 0.41. These estimates suggest that at low population sizes and in the absence of anthropogenic mortality, one alewife can produce about 21.3 age-3 recruits throughout its life and that the carrying capacity for a typical alewife population is about 55 t·km^{-2} of nursery area. We will also use these distributions as informative priors when estimating reference F values in a later section.

Maximum likelihood estimation of F_{msy}

The F_{msy} may be estimated using surplus production models, SR models for semelparous species, delay difference models, and age-structured production models (Quinn and Deriso 1999). Here, we estimate F_{msy} using a production model for alewife consisting of three parts: an SR relationship, an SPR model, and a YPR model. Gibson and Myers (2003*a*) found that the Beverton–Holt SR model provided a consistently better fit to alewife SR data than did the Ricker model. The Beverton–Holt SR model gives the number of recruits (defined here as the number of offspring that survive to age 3) in year $t + 3$, R_{t+3}, as a function of the spawning biomass in year t, SSB_t.

$$(1) \qquad R_{t+3} = \frac{\alpha SSB_t}{1 + (\alpha SSB_t / R_0)}$$

Here, α is the slope at the origin and in the deterministic model is the maximum rate at which spawners can produce recruits at low population sizes in a single year (Myers et al. 1999). This term, together with the SPR model (see below), determines the maximum annual reproductive rate (the maximum rate at which spawners produce replacement spawners annually) as well as the maximum lifetime reproductive rate, defined as the maximum rate at which spawners can produce replacement spawners throughout their lives (Myers et al.

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1999). In this model, R_0 is the asymptotic recruitment level and is the limit approached by R_t as SSB_t approaches infinity (note that the Beverton–Holt model is often written in terms of the half-saturation constant, K, which is related to R_0 by $R_0 = \alpha K$). Parameter estimates may be obtained using maximum likelihood. Assuming a lognormal error structure (Myers et al. 1995), the log-likelihood is given by

$$(2)\quad \ell(\alpha, R_0, \sigma) = -n \log \sigma\sqrt{2\pi} - \sum \log R_t - \frac{1}{2\sigma^2} \times \sum \log\left(\frac{R_t}{g(\mathrm{SSB}_t)}\right)^2$$

where SSB_t and R_t are the observed spawner biomass and recruitment data, $g(SSB_t)$ is the Beverton–Holt SR function, σ is the standard deviation of a normal distribution prior to exponentiation, and n is the number of paired SR observations.

The second model component is the SPR model, which gives the rate at which recruits produce spawners as a function of fishing mortality (Shepherd 1982; Mace and Sissenwine 1993; Mace 1994). For in-river alewife fisheries (Gibson and Myers 2003*a*), this is

$$(3)\quad \mathrm{SPR}_F = \sum_{a_{min}}^{a_{max}} \mathrm{SS}_a w_a \exp(-F)$$

where

$$\mathrm{SS}_1 = m_1$$

$$\mathrm{SS}_4 = \mathrm{SS}_3 \exp[-(M^{adult} + F)] + (1 - m_3)\exp(-M^{juv})m_4$$

$$\mathrm{SS}_5 = \mathrm{SS}_4 \exp[-(M^{adult} + F)] + (1 - m_3)(1 - m_4)\exp(-2M^{juv})m_5$$

$$\mathrm{SS}_6 = \mathrm{SS}_5 \exp[-(M^{adult} + F)] + (1 - m_3)(1 - m_4)(1 - m_5)\exp(-3M^{juv})m_6$$

$$\vdots$$

$$\mathrm{SS}_{a_{max}} = \mathrm{SS}_{a_{max}-1} \exp[-(M^{adult} + F)] + (1 - m_3)(1 - m_4)\ldots(1 - m_{a_{max}-1}) \times \exp[-(a_{max} - 3)M^{juv}]m_{a_{max}}$$

Here, a is the age of the fish, m_a is the probability that a fish that is alive at age a will mature at that age, M^{adult} and M^{juv} are as the instantaneous natural mortality rates for adult and juvenile alewife, respectively, and w_a is the weight at age. These values are fixed constants in this analysis, although the decision theoretic methods presented herein could be extended to include uncertainty in these parameters.

In-river alewife fishing seasons are typically relatively short (about a month) with the majority of the catch being taken during a couple weeks. As a result, the effects of natural and fishing mortality occurring concurrently can be ignored when estimating the YPR. The YPR for a given F (YPR_F) is thus found analogously to the SPR.

$$(4)\quad \mathrm{YPR}_F = \sum_{a_{min}}^{a_{max}} \mathrm{SS}_a w_a [1 - \exp(-F)]$$

For a given value of F, the spawning biomass produced by a given number of recruits in year t (throughout their lives) is $SSB = SPR_F R_t$. Equilibrium spawning biomass and recruitment levels may be found by solving this equation for R_t and substituting the result in the SR model (Quinn and Deriso 1999). For a given α and R_0 pair, the equilibrium yield, Y^*, can be calculated for each value in a set of F values and F_{msy} can be found using a search over the set to find the fishing mortality where Y^* is maximized. If the MLEs of α and R_0 are used, the MLE of F_{msy} is obtained. This is the most common method of estimating F_{msy} but does not include uncertainty in the SR parameters in the selection of a reference F.

The data for both alewife populations show considerable variability about the fitted SR model (Fig. 1). For the Gaspereau River population, all observed SSBs are low relative to the estimated equilibrium unfished spawner biomass, and all but three are below SSB_{msy}. The SR parameter estimates ($\alpha = 96.1$, $R_0 = 1.6 \times 10^6$, and $\sigma = 0.42$) obtained from these data appear biologically realistic, although given the limited range of the observed spawner biomasses, at least the estimate of the asymptotic recruitment level is questionable. The SSBs for the Miramichi alewife population have a greater range than for the Gaspereau River population, but the data exhibit greater variability about the fitted SR relationship. The SR parameter estimates for this population ($\alpha > 1 \times 10^9$, $R_0 = 7.4 \times 10^6$, and $\sigma = 0.94$) are biologically unrealistic: the estimate of α exceeds the fecundity of the fish, and the parameter estimates suggest that a spawner biomass of 10 g can produce half the recruitment of a spawner biomass of a million kilograms. Estimates of F_{crit} (the fishing mortality rate that drives the population to extinction) and F_{msy} from the Miramichi data exceed 5.0, suggesting that the population cannot be overfished, and are simply not believable.

Evaluating uncertainty in F_{msy}

These examples illustrate some of the problems that may be encountered when deriving reference F values from noisy SR data. In the case of the Miramichi River population, the SR parameter estimates and resulting reference points are clearly unrealistic. Nonetheless, management advice often has to be provided when only data of this type are available. Plausible estimates are obtained for the Gaspereau River population, although they may be questionable given the limited range of the data.

The plausibility of an individual parameter estimate can be assessed by examining its log profile likelihood (Davison and Hinkley 1997). The log profile likelihood for α, $\ell_p(\alpha)$, is

$$(5)\quad \ell_p(\alpha) = \max_{R,\sigma} \ell(\alpha, R_0, \sigma)$$

The MLE for α occurs where ℓ_p is maximized. The plausibility of other possible values of α is evaluated by comparing their log profile likelihoods with the maximized log profile likelihood. A likelihood ratio based 95% confidence interval for α is

$$(6)\quad [\alpha : 2[\ell_p(\alpha^{MLE}) - \ell_p(\alpha)] \le \chi^2_1(0.95)]$$

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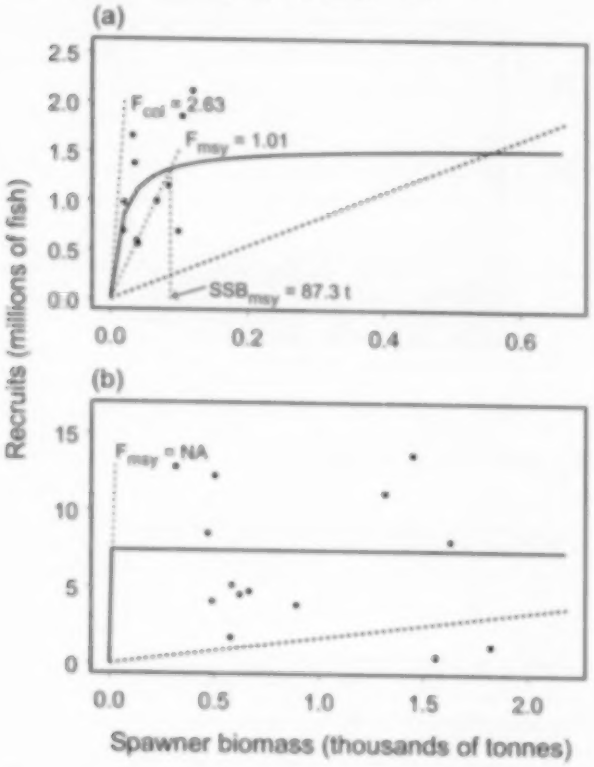
Fig. 1. Beverton–Holt spawner–recruit (SR) models (solid line) and production model reference points for the (*a*) Gaspereau River and (*b*) Miramichi River alewife populations. The SR models are the maximum likelihood fits assuming lognormal errors. The broken line is the replacement line in the absence of fishing mortality. The slope of the SR model at the origin was essentially infinite for the Miramichi population, and reference points could not be estimated for that population. F_{crash}, fishing mortality rate that drives the population to extinction; F_{msy}, fishing mortality rate that produces maximum sustainable yield; SSB_{msy}, spawning biomass at maximum sustainable yield; NA, not available.



The profile likelihood and the associated 95% confidence interval for R_0 were found similarly and for F_{msy} by mapping from the profile likelihood for α to F_{msy} using the production model.

The log profile likelihood for α for the Miramichi population is ramped: the lower bound of the 95% confidence interval for α is determined, but the MLE and its upper bound are essentially infinite (Fig. 2). For the Gaspereau population, the MLE of α and the lower bound of its 95% confidence interval may be estimated, but $\ell_p(\alpha)$ decreases only very slightly above the MLE. The asymptotic recruitment level is better determined by the data, although the upper and lower 95% confidence limits differ by a factor of about 5 times. The pattern for F_{msy} is similar to that of α; only the lower bound is determined by the data. Clearly, for data sets similar to these, the MLEs of the SR parameters and the associated estimates of F_{msy} are not good reference points for fishery management.

The log likelihood surfaces for α and R_0 (Fig. 2) provide a basis for assessing the plausibility of pairs of parameter values. The surfaces for both the Gaspereau and Miramichi populations show an L-shaped ridge, along which the likelihood changes only slightly. This implies that the probability of observing the data is similar, given either low values of α and high values of R_0 or high values of α and low values of R_0. One cannot choose between these scenarios on the basis of the data, and these surfaces again show the considerable uncertainty associated with the MLE of F_{msy}.

Estimating reference *F* values that include SR parameter uncertainty

For both the Miramichi River and Gaspereau River alewife populations, there are plausible values of α (not significantly different from the MLE of α at a 95% confidence level) for which there exists the possibility that the asymptotic recruitment level is substantially higher than its MLE. The data therefore do not preclude the possibility of larger recruitments, suggesting that the subsequent yield could potentially increase if the fishing mortality rate were set below the MLE for F_{msy}. The data also suggest that larger recruitments are less plausible at the MLE for α than at lower values for this parameter. An appropriate reference *F* should not preclude the possibility of achieving larger catches, particularly if the reference rate is not significantly different from the MLE of F_{msy}. In this section, we demonstrate the two alternative methods of deriving reference *F* values that include SR parameter uncertainty: the use of the mode of the marginal probability density for α to determine F_{mmy} and finding the fishing mortality rate that maximizes the expectation of the catch, $F_{max E[Y]}$.

We begin by selecting a parameter space, Ω, for the SR model with two dimensions: α and R_0. Any point in this parameter space may be viewed as a separate hypothesis about the SR relationship for each population. We used $\alpha = 1/\mathrm{SPR}_{F=0}$ as the lower limit for α for each population. Below this limit, the population would go extinct because reproduction would not be sufficient to offset natural mortality. We set the upper bound for α at 250. We used the first and 99th percentiles of the random effects distribution of R_0 for the bounds on R_0. The joint Bayesian posterior distribution is given by

$$(7)\qquad p(\alpha, R_0) = \begin{cases} \dfrac{L(\mathbf{R}|\mathbf{S}, \alpha, R_0)p(\alpha)p(R_0)}{\iint_{\Omega} L(\mathbf{R}|\mathbf{S}, \alpha, R_0)p(\alpha)p(R_0)\mathrm{d}\alpha\,\mathrm{d}R_0}, & \alpha, R_0 \in \Omega \\ 0 & \text{otherwise} \end{cases}$$

where $L(\mathbf{R}|\mathbf{S},\alpha,R_0)$ is the probability of observing the data for a given pair of parameter values. The prior probalities, $p(\alpha)$ and $p(R_0)$, are the probabilities for alternative values for the parameters before considering data for the population under study. In this section, we assume uniform priors over the intervals above; more informative priors are considered in a later section. The marginal probability distribution for α is calculated from the posterior distribution as

$$(8)\qquad p(\alpha|p(\alpha,R_0)) = \int p(\alpha,R_0)\,\mathrm{d}R_0$$

The mode of the resulting probability density provides an alternative estimate of α that is used to calculate F_{mmy}.

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Fig. 2. (*a*) Contour plots showing the joint log likelihood surface for the slope at the origin of the spawner–recruit (SR) model and the asymptotic recruitment level for the Gaspereau River and Miramichi River alewife populations. The square indicates the point at which the log likelihood is maximized (not available for the Miramichi population). The contour interval is –1 moving away from this point. The grey-shaded region shows the likelihood-based 95% joint confidence region for the parameters. Profile log likelihoods (solid lines) are shown for (*b*) the slope at the origin, (*c*) the asymptotic recruitment level, and (*d*) the fishing mortality rate at maximum sustainable yield (F_{msy}), the latter obtained from the profile likelihood for the slope at the origin of SR model. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections of the broken lines and the profile likelihoods show likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for the slope at the origin or F_{msy} for either population.

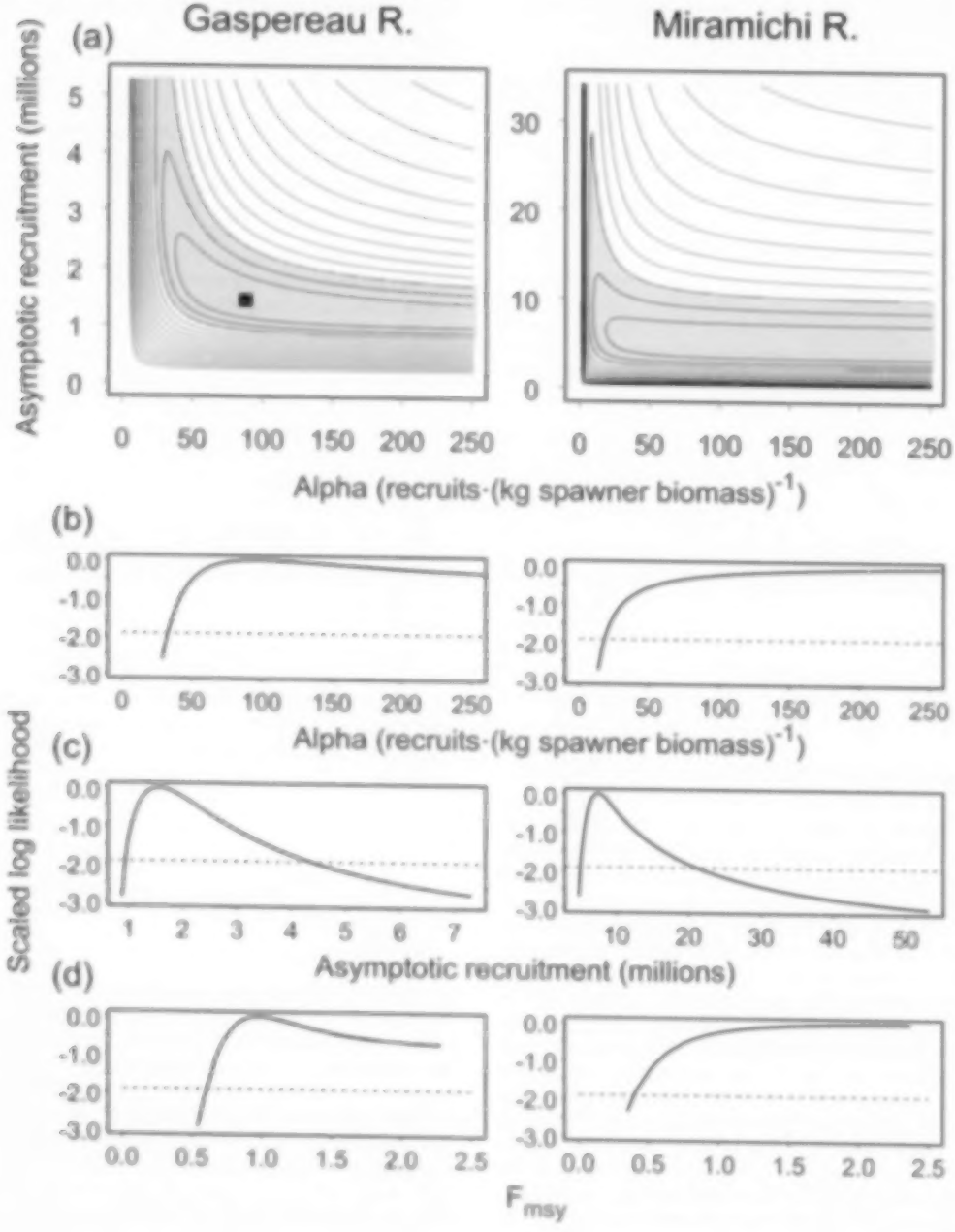

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Table 2. Reference exploitation rates for two alewife populations in the Maritime Provinces, Canada, estimated without spawner–recruit (SR) data, using population-specific SR data, and using SR data from other populations.

Reference point	Exploitation rate	
	Gaspereau River	Miramichi River
No data		
$F_{max E[Y]}$ (uniform bounded probability surface)	0.61	0.63
Population-specific data only		
F_{msy} (maximum likelihood estimate)	0.63	>0.99
F_{marg} (mode of the marginal likelihood for α)	0.56	0.77
$F_{max E[Y]}$ (joint likelihood for α and R_0)	0.61	0.68
Data from other populations only		
F_{msy} (mode of joint prior distribution for α and R_0)	0.56	0.53
F_{marg} (mode of the marginal probability density for α based on the joint prior distribution)	0.56	0.53
$F_{max E[Y]}$ (joint prior distribution for α and R_0)	0.56	0.53
Combined data		
F_{msy} (mode of joint posterior distribution for α and R_0)	0.56	0.53
F_{marg} (mode of the marginal probability density for α based on the joint posterior distribution)	0.56	0.53
$F_{max E[Y]}$ (joint posterior distribution for α and R_0)	0.56	0.53

Note: Estimates are obtained by using (*i*) the mode of joint likelihood or probability distributions (F_{msy}), (*ii*) the marginal likelihood or probability density for α (F_{marg}), or (*iii*) by finding the fishing mortality rate that maximizes the expectation of the catch ($F_{max E[Y]}$). msy, maximum sustainable yield.

For a given F, the expectation of the equilibrium yield is given by

$$(9) \qquad E[Y^*(F)] = \iint Y^*(F,\alpha,R_0)p(\alpha,R_0)\,dR_0\,d\alpha$$

where $Y^*(F,\alpha,R_0)$ is the equilibrium yield as a function of the fishing mortality rate, α, and R_0 and $p(\alpha,R_0)$ is the posterior density evaluated at α and R_0. The fishing mortality rate that maximizes the expectation of the yield is then

$$(10) \qquad F_{max E[Y]} = \underset{F}{\operatorname{argmax}}\ E[Y^*(F)]$$

Estimates of $F_{max E[Y]}$ could be obtained without SR data simply by assuming that all values for the SR parameters within some range were equally probable. Plausible estimates were obtained using this method, although the estimates are sensitive to the assumed range. When the population-specific data are included, the estimates of F_{marg} and $F_{max E[Y]}$ are less than the MLEs of F_{msy} for both the Gaspereau and Miramichi alewife populations (Table 2). While the MLE of F_{msy} for the Miramichi River population was essentially infinite, plausible estimates of F_{marg} and $F_{max E[Y]}$ could be obtained. For the Gaspereau River population, the exploitation rate corresponding to F_{marg} was 0.7 lower than that corresponding to the MLE of F_{msy}. The exploitation rate corresponding to $F_{max E[Y]}$ was between these values.

Comparison of F_{msy}, F_{marg}, and $F_{max E[Y]}$

Both F_{marg} and $F_{max E[Y]}$ provided estimates of reference F values that were lower than F_{msy} for Gaspereau River alewife. These reference points could also be calculated for the Miramichi River population, for which the estimate of F_{msy} was essentially infinite. Additionally, these reference points are intuitively appealing, because uncertainty in the SR relationship is explicitly included in their estimation. In this section, we compare the performance of these three reference points using a Monte Carlo simulation model.

The simulation model is based on the production model used to estimate F_{msy}. We ran simulations for 25 combinations of α (values: 10, 25, 50, 100, 250) and σ (0.1, 0.3, 0.5, 0.7, 0.9). A constant R_0 was used for all simulations. For each combination, we simulated 500 SR data sets, randomly choosing 20 spawner biomasses between zero and the unfished equilibrium spawner biomass for each simulation. Recruitments were assigned to each spawner biomass by randomly selecting a value from a lognormal distribution with its mean determined by the SR function

$$(11) \qquad R_i = \frac{\alpha \mathrm{SSB}_i}{1+\dfrac{\mathrm{SSB}_i}{K}} \exp\left(\varepsilon_i\sigma - \frac{\sigma^2}{2}\right)$$

where

$$\varepsilon_i \sim N(0,1)$$

The same random numbers were used for each set of 500 simulations to ensure that any differences detected were not an artefact of the random number generation. The reference points F_{msy}, F_{marg}, and $F_{max E[Y]}$ were calculated for each data set as described in the previous sections.

At low levels of recruitment variability, the three references points performed similarly (Fig. 3). However, both F_{marg} and $F_{max E[Y]}$ consistently underestimated the true F_{msy} at higher levels of σ, whereas the MLE of F_{msy} was the least biased estimator of the true F_{msy}. However, the MLE was the most variable estimator, at times substantially overestimating or underestimating the true F_{msy}. At higher levels of α and σ, $F_{max E[Y]}$ had the least variability.

Do the benefits of least biasness outweigh the cost of high variability when choosing a method of estimating a reference F? We addressed this question by comparing the equi-

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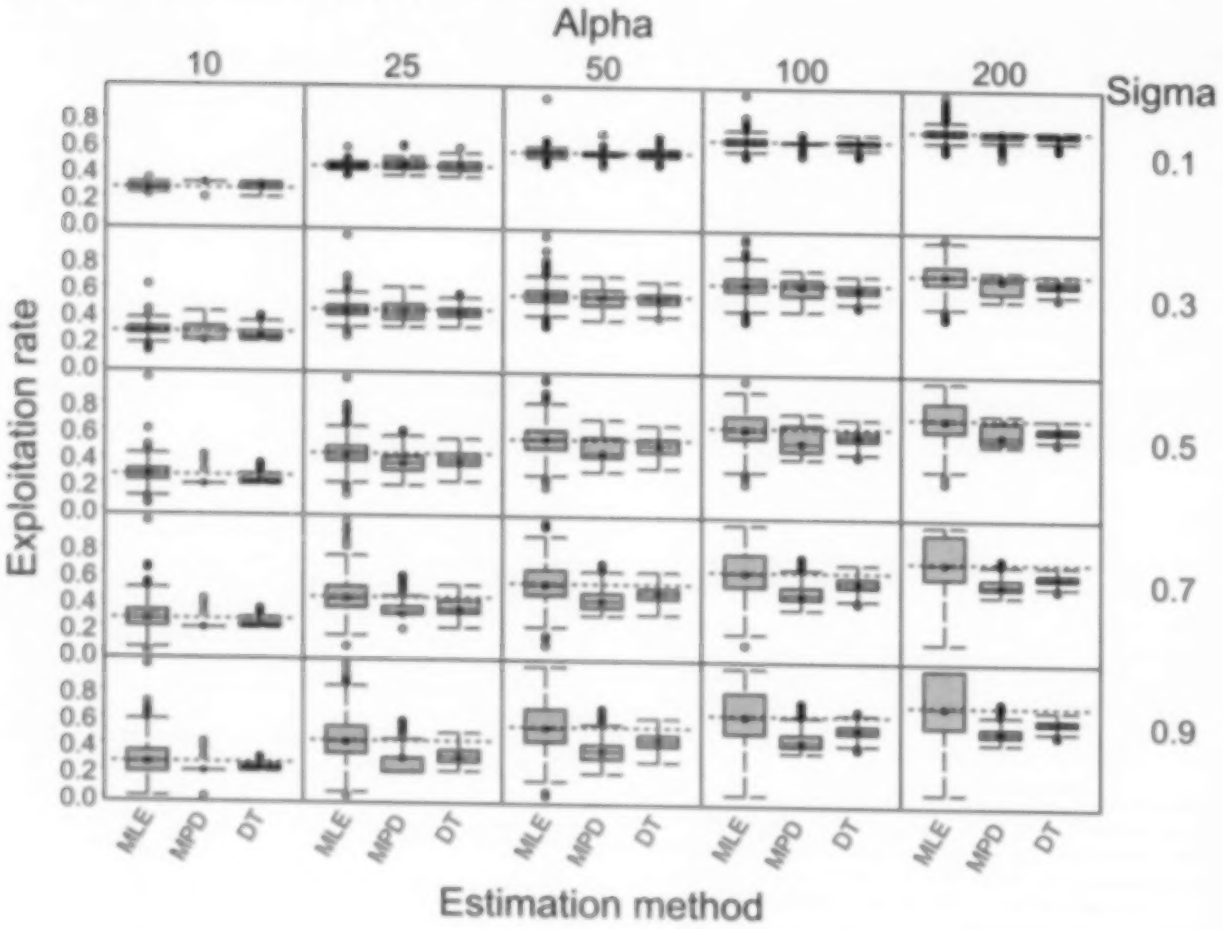
Fig. 3. Summary of the simulation results comparing reference fishing mortality rates estimated using maximum likelihood estimation (MLE), the mode of the marginal probability density (MPD), and a decision theoretic model (DT). The resulting reference points are referred to as F_{msy}, F_{marg}, and $F_{max E[Y]}$, respectively. The box plots show the distributions of the estimated reference fishing mortality rates for 500 simulated spawner–recruit (SR) data sets for each combination of α and σ. The median value is indicated with a point and the grey-shaded region shows the interquartile range. The whiskers are drawn to the nearest value within 1.5 times the interquartile range. The broken line gives the true F_{msy} for the simulated dynamics.



librium yield, spawner biomass, YPR, and SPR that would result if the estimated reference F values were applied to a population with the dynamics used to simulate the data. Using the case of $\alpha = 50$ and $\sigma = 0.9$ as an example, about 25% of the populations would be highly overexploited if fished at the estimated MLE of F_{msy}, and 13.4% of the populations would be fished to extinction at this rate (Fig. 4). None of the populations would be highly overexploited when fished at F_{marg} or $F_{max E[Y]}$ (Fig. 4). Differences in mean equilibrium yield, spawner biomass, YPR, and SPR resulting from the three reference F values were small at low levels of recruitment variability but increased as variability increased (Fig. 5). On average, $F_{max E[Y]}$ produces higher yields than either F_{msy} or F_{marg} while maintaining spawner biomasses that are on average higher than F_{msy} but slightly lower than F_{marg} (Fig. 5). In the example of $\alpha = 50$ and $\sigma = 0.9$, the mean equilibrium yield obtained by fishing at $F_{max E[Y]}$ exceeded the mean equilibrium yield obtained by fishing at F_{msy} by a factor of 1.19 while maintaining spawner biomasses that were higher by a factor of 1.34. The $F_{max E[Y]}$ typically produced YPR values between those of F_{msy} and F_{marg}, although these differences were small (Fig. 5). The F_{marg}, the most conservative reference point, maintained the highest SPR levels.

Including information from other populations

The decision theoretic approach of maximizing the expectation of the yield is easily extended to include information from other populations. We used the random effects distribution for the log of the maximum lifetime reproductive rate and for the log of the adult carrying capacity obtained by Gibson and Myers (2003*b*) to derive empirical priors for α and R_0. The MLE of the random effects distributions, known as MLE priors (Efron 1996), are used in the empirical Bayes

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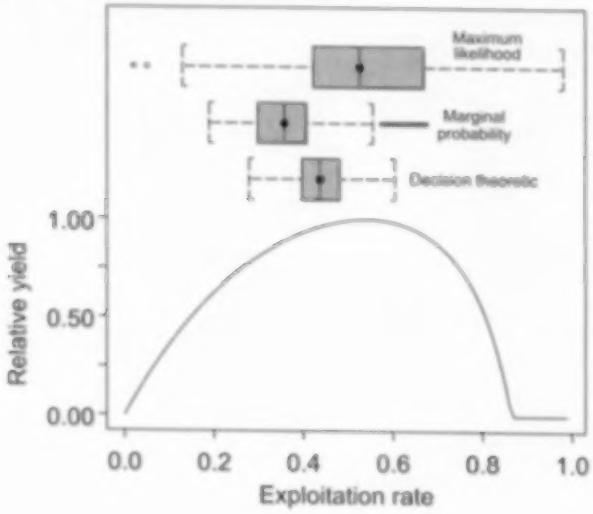
Fig. 4. Summary of the simulation results for values of $\alpha = 50$ and $\sigma = 0.9$. The solid line gives the known equilibrium yield, scaled to a maximum of 1, as a function of the exploitation rate. The box plots show the distribution of the reference fishing mortality rates estimated from 500 simulated spawner–recruit (SR) data sets using the three methods. The maximum likelihood method produces the MLE of F_{msy}, the marginal probability method uses the mode of the marginal probability density for the maximum reproductive rate to obtain a reference F (F_{marg}), and a reference F is found using the decision theoretic method by maximizing the expected yield ($F_{max E[Y]}$). For each method, the solid line is the median value and the grey-shaded region shows the interquartile range. The whiskers are drawn to the nearest value within 1.5 times the interquartile range. Points beyond these limits are plotted as open circles.



analysis that follows. The priors are obtained by transforming the random effects distributions back to the original scale, dividing both random effects distributions by $SPR_{F=0}$, and multiplying the carrying capacity distribution by the amount of nursery habitat available for the population under study. These steps convert the distribution for α from units of lifetime spawners per spawner to recruits per unit biomass, and the distribution for carrying capacity from units of biomass per unit area to numbers of recruits. The resulting priors then contain information about the distribution of the SR parameters at the species level obtained by analyzing data from other alewife populations.

The resulting empirical prior probability densities for α and R_0 for alewife are shown together with the likelihood surface for these parameters for Gaspereau River alewife (Fig. 6), providing a basis for assessing the plausibility of the estimates of α and R_0 for the Gaspereau River alewife population. The MLE of α is high relative to the mode of the prior for α at the species level, whereas the prior for R_0 suggests that we may be underestimating R_0 using only the population-specific data. The population-specific data do not preclude the possibility of very high asymptotic recruitment levels at lower values of α, although the prior for R_0 indicates that these high asymptotic recruitment levels are not very plausible given the species-level information. A different pattern is evident for the Miramichi River alewife population (Fig. 6). The likelihood surface suggests that R_0 is reasonably estimated from the population-specific data even though the data are largely uninformative about α. However, comparison with the priors suggests that the estimate of R_0 obtained for this population is low relative to that of other alewife populations.

During the estimation of $F_{max E[Y]}$ in the preceding section, uniform bounded priors were assumed for $p(\alpha)$ and $p(R_0)$. The priors distributions for α and R_0 obtained from the meta-analysis are more informative alternatives for $p(\alpha)$ and $p(R_0)$ and enter directly into the estimation of $F_{max E[Y]}$ through the calculation of the Bayesian joint posterior distribution, $p(\alpha, R_0)$, shown in eq. 13. When the informative priors are used, the estimates of the exploitation rate corresponding to $F_{max E[Y]}$ for Gaspereau River alewife are reduced from 0.61 (uniform bounded prior) to 0.56 (Table 2). For the Miramichi River population, the estimate is reduced from 0.68 to 0.53. For both populations, the prior for α has the greatest influence on the estimates of the reference F values. The estimates obtained using only the data from the other populations and using the combined data are the same (Table 2) because the population-specific data are relatively uninformative about the true value of α in comparison with this prior (Fig. 6).

Discussion

Despite being embedded in the management objectives of many organizations and countries (Quinn and Deriso 1999; Mace 2001), the concept of MSY has been the target of much criticism (e.g., Larkin 1977). These criticisms typically fall into three categories: problems with its implementation, its appropriateness as a management goal, and problems with its estimation (Punt and Smith 2001). Implementation problems are not specific to MSY but apply to any management objective. In recent years, the role of MSY as a management objective has undergone a shift as a result of the development of precautionary and ecosystem-based approaches to fisheries management (Mace 2001). While the difficulty with the estimation of F_{msy} remains a valid criticism of MSY, we have demonstrated in this paper that better reference fishing rates can be obtained by using the decision theoretic approach of maximizing the expected yield and by including data from other populations when estimating a reference F.

When choosing any model-based reference point, an underlying mathematical model that reflects the fish population dynamics is also selected. Caddy and Mahon (1995) suggested that when selecting a reference point, rather than simply choosing the one with the best theoretical underpinnings, a more appropriate criterion may be picking the reference point that provides conservative advice under conditions of uncertainty. In our examples, although maximum likelihood was the least biased of the methods examined here, it provided the highest estimates for a reference F and lower average yields than the method of maximizing the expected yield, particularly when the SR data are noisy. The method of maximizing the expected yield is therefore more precautionary than the maximum likelihood method from both a conservation perspective (lower fishing mortality rates and higher spawner biomasses) and that of maximizing yield.

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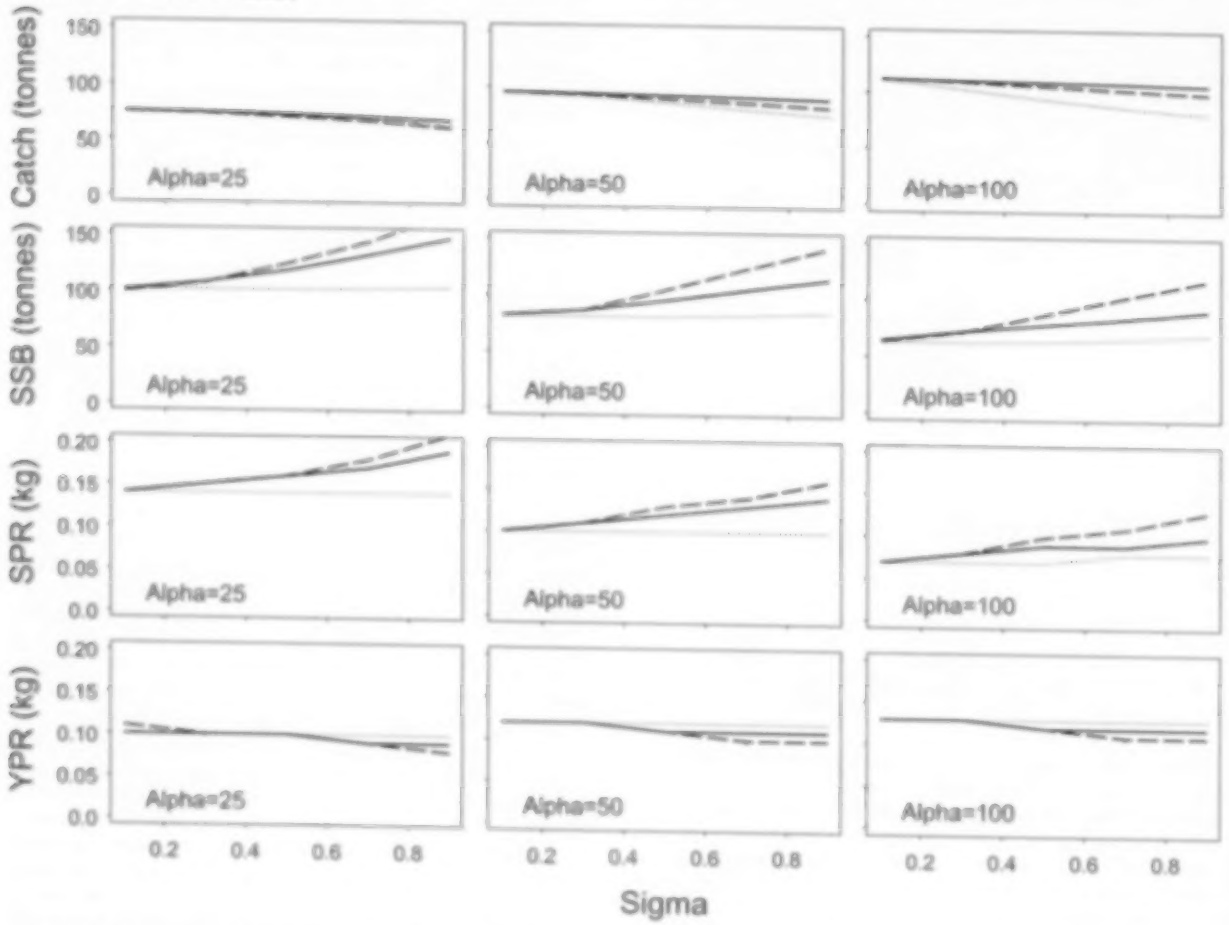
Fig. 8. Comparison of the mean equilibrium catch, spawner biomass (SSB), spawning biomass per recruit (SPR), and yield per recruit (YPR) obtained by fishing at three estimated reference fishing mortality rates. Equilibrium values were calculated by applying the estimated reference fishing mortality rates for each data set to the known dynamics used to simulate the data and are the means of 500 simulated spawner–recruit (SR) data sets for each combination of the SR slope at the origin (α) and recruitment variability (σ). The dotted line shows the values obtained when the maximum likelihood estimate (MLE) of α is used to estimate the fishing mortality rate that produces maximum sustainable yield (F_{msy}); the broken line shows the values obtained when the mode of the marginal probability density is used to estimate a reference F (F_{marg}); and the solid line shows the values obtained by fishing at a rate that maximizes the expectation of the yield $F_{max[E]}$.



In our simulations, the fishing mortality rate that maximized the expectation of the yield could be reasonably estimated from all data sets and showed much lower variability than the MLE of F_{msy}. In the case of the Miramichi River alewife, the MLE of F_{msy} was essentially infinite, whereas the exploitation rate that maximized the expected yield was 0.68. This estimate is slightly higher than the average exploitation rate at MSY for alewife (0.65) reported by Crecco and Gibson (1990) and is within the range of values reported by Gibson and Myers (2003*b*). However, using a life history based simulation model, the latter authors found that an exploitation rate of about 0.40 for in-river alewife fisheries produced more than 90% of MSY and suggested this to be a reasonable limit given that no allowances were made for factors such as implementation uncertainty. The inclusion of information from other populations through the use of informative priors lowered the estimated reference exploitation rates to 0.53 for the Miramichi population, providing a more conservative but reasonable reference F given the above results. Additionally, we did not obtain infinite estimates of the reference F values obtained from the mode of the marginal probability density or by maximization of the expected yield in any of the 12 500 simulated data sets in this study, although the estimates of infinite slopes at the origin (and the MLE of F_{msy}) were obtained for many of the simulated data sets. These results illustrate the problems with estimating F_{msy} using maximum likelihood, indicate that reasonable reference F values may be obtained by maximizing the expected yield even when the SR data exhibit considerable variability, and show that inclusion of information from other populations can also improve the resulting estimates.

While maximization of the yield performed well in our simulations, caution is warranted when using data with a limited spawner biomass range. For the Miramichi River popula-

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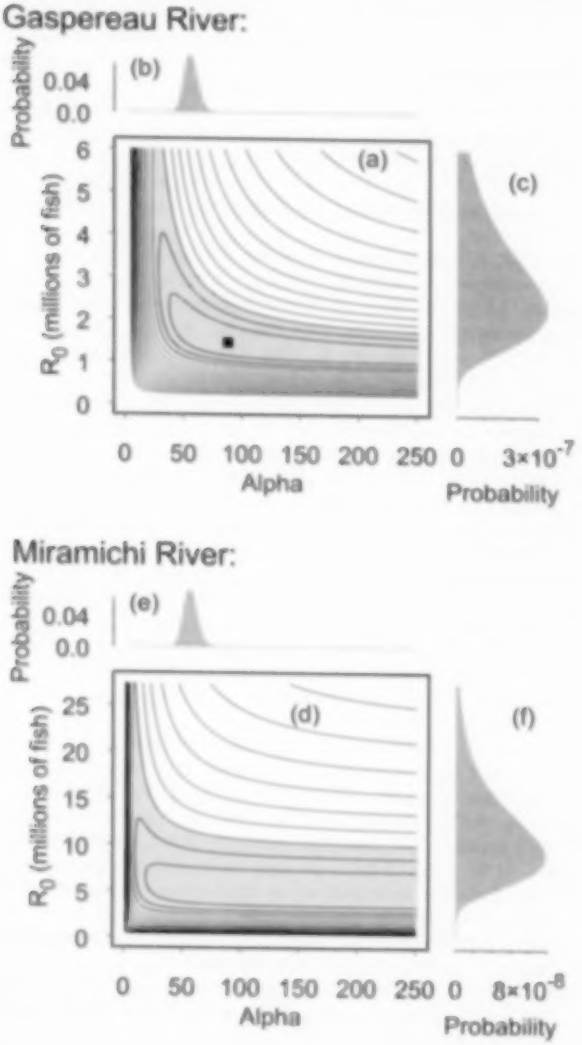
Fig. 6. Comparison of (*a* and *d*) the joint log-likelihood surface for the slope at the origin and the asymptotic recruitment level with the random effects distributions for (*b* and *e*) the slope at the origin and (*c* and *f*) the asymptotic recruitment level for two alewife populations. The random effects distributions are derived from a meta-analysis of eight alewife populations and depict the distribution of the spawner–recruit (SR) parameters for alewife at the species level and are scaled by the amount of nursery area available for these populations. The square in the log-likelihood surface shows the point where the log-likelihood is maximized. The contour interval is –1 moving away from this point. The grey-shaded region shows the likelihood ratio based 95% confidence region for the parameters.



tion, the exploitation rate that maximized the expectation of the yield from the population-specific data was higher than when information from other populations was included. As shown in this study, R_0 appears to be reasonably estimated for this population but is low in comparison with other populations. While it is possible that Miramichi alewife have a higher maximum reproductive rate and lower carrying capacity than other alewife populations, a more precautionary explanation is that this result reflects limitations of the data not overcome by maximizing the expected yield using only the population-specific data. When SR data have a limited range of spawner biomasses, R_0 may appear to be reasonably well estimated when in fact the estimate only reflects the average recruitment in the data series. This is the case with the Miramichi alewife data as evidenced by the infinite estimate of the maximum rate that spawners produce recruits. In these instances, the resulting reference F obtained by maximizing the expected yield may still be high relative to the true F_{msy}. Comparison with parameter estimates from similar populations provides a method to detect this problem. Alternatively, SR data from several populations can be standardized so that they can be plotted on the same scale. When this is done, populations with data that are dissimilar to data for other populations are immediately evident (Myers et al. 2001; Gibson and Myers 2003*a*). This method can also be used to detect populations for which data is insufficient to estimate R_0.

At least in our examples, the method of maximizing the expectation of the yield clearly outperformed the maximum likelihood method of estimating F_{msy}. This finding leads to the suggestion that model fitting criteria based on management objectives may outperform those based solely on statistical criteria such as least biasness. However, in our examples, reference F values obtained from the mode of the marginal probability for the SR slope at the origin (F_{marg}) also produced higher average yields and spawner biomasses than reference F values obtained by maximum likelihood even though the F_{marg} showed the greatest bias. Also using simulations, Nielsen and Lewy (2002) found that a Bayes estimate of spawning biomass in an age-structured assessment model outperformed the MLE. In their example, the Bayes estimate showed less bias but was based on the posterior mean rather than the mode. Both of these analyses demonstrate the advantages of obtaining parameter estimates from the marginal probability density as opposed to maximum likelihood.

One of the most striking outcomes of our analyses is the observation that when F_{msy} was estimated from noisy SR data using maximum likelihood, a portion of the populations could be fished to extinction if the reference F was implemented. In 13.4% of the $\alpha = 50$ and $\sigma = 0.9$ simulations, the estimate of F_{msy} exceeded the fishing mortality rate that would drive the population to extinction and would have serious consequences for the population if used as a management target. In instances where the estimate of F_{msy} is essentially infinite, the estimate is obviously wrong and would not be used as a basis for management advice. The more serious problem occurs at low α values when it may not be obvious when the MLE of F_{msy} exceeds the productive capacity of the population. Based on our simulations, this problem is alleviated by changing the optimization criteria for estimating the reference F: none of the simulated populations would be fished at a rate that causes extinction if fished at the rate obtained by maximizing the expectation of the yield.

The use of meta-analysis is becoming more common in fisheries science (e.g., Harley and Myers 2001; Chen and Holtby 2002; Dorn 2002). For many species of fish, proba-

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bility distributions for the maximum reproductive rate have been derived at the species and family levels (Myers et al. 1999) and for categories based on life history strategies (Myers et al. 2002). In this paper, we have shown how these distributions can be used to evaluate reference points based on stock-specific analyses, to place bounds on the range of plausible values for the SR parameters (also see Brodziak 2002), and be incorporated directly into reference point estimation. In our analyses, the priors for α and R_0 were much more informative than the data for either population and therefore dominated the reference point estimation procedure. Gibson and Myers (2003*b*) did not preclude the possibility that the variance for α was underestimated in their analysis. Increasing the variance on the prior for α without changing its mean decreases the resulting reference F obtained by maximizing the expected yield.

The idea that reference points are more conservative when uncertainty is included in their estimation is not new. Ludwig and Walters (1982) found that in an active adaptive policy, inclusion of parameter uncertainty lead to higher target spawning escapements, although lower escapements could also lead to higher long-term yields if they resulted in a reduction in parameter uncertainty. Walters and Pearse (1996) concluded that uncertainty in stock size estimates would significantly lower allowable catches as low-risk management policies are adopted. Decision theory provides a method for incorporating uncertainty into the decision framework through the use of a loss function. Finding the fishing mortality rate that maximizes the expected yield provides a decision theoretic reference point with a risk-neutral loss function because the magnitude of the equilibrium catch is used in its calculation. Risk-adverse approaches may also be implemented without substantial modifications to the method by weighting or transforming the yield prior to maximizing the expected yield.

Both the Miramichi River and Gaspereau River alewife populations have YPR relationships that are ramped (Gibson and Myers 2003*b*). The method of maximizing the expected yield given uncertainty in the SR parameters is most appropriate for fisheries similar to the fisheries on these rivers (a nonselective fishery on fish that are relatively full grown prior to recruiting to the fishery). For populations with a well-determined F_{max} (typically a fishery that catches fish over a wider size range), assumptions about the selectivity pattern, growth, and survival will have greater influence on F_{msy} than in our examples. If the uncertainly associated with these parameters is quantified, it can also be included when estimating a reference F using the method of maximizing the expected yield.

In summary, the analyses presented herein indicate that using decision theoretic methods that evaluate the quantities of interest, i.e., fishing mortality and yield, outperforms more indirect methods, i.e., using MLE of SR parameters to derive the fishing mortality rate that produces MSY. The decision theoretic reference F was more conservative and produced higher yields and spawner biomasses while reducing the probability of under- or over-exploiting the population in comparison with the MLE of F_{msy}. Additionally, when data from other populations are available, they can be either used to assess the plausibility of parameter estimates or incorporated directly into the reference point estimation process. In these ways, the use of fishery reference points as guide to fishery management can be improved.

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Relationship of fish catch and composition to water quality in a suite of agriculturally eutrophic lakes

Christopher J. Egertson and John A. Downing

Abstract: We examined the fish community, water quality, and morphometry of 32 agriculturally eutrophic lakes. Our purpose was to explore the relationships between eutrophication and fish catch per unit effort by weight ($CPUE_w$) and fish community composition of the six most important species in this suite of the world's most nutrient-rich lakes. We found that the $CPUE_w$ of the sum of all species increased with lake trophic status measured as chlorophyll *a* ($r = 0.45$, $p < 0.009$). By dissecting total fish $CPUE_w$ into individual species and functional groups, we found that only common carp (*Cyprinus carpio*) and benthivore $CPUE_w$ increased significantly with trophic status ($p < 0.03$ and 0.001, respectively). Sport fish (principally piscivores) decreased as a proportion of total $CPUE_w$ by approximately 50%, while benthivores, primarily common carp, increased by approximately 80% over an increase in chlorophyll *a* from 10 to 100 μg·L^{-1}. Common carp $CPUE_w$ was correlated with and may have a negative influence on $CPUE_w$ of bluegill (*Lepomis macrochirus*) and black crappie (*Pomoxis nigromaculatus*) and a positive influence on white crappie (*Pomoxis annularis*). Our study suggests that species other than benthivores may be unable to exploit increased energy availability in hypereutrophic systems or are competitively excluded from using this increased production.

Résumé : Nous avons examiné la communauté de poissons, la qualité de l'eau et la morphométrie de 32 lacs rendus eutrophes par l'agriculture. Notre objectif est d'étudier la relation entre l'eutrophisation, la capture de poissons (en masse) par unité d'effort ($CPUE_w$) et la composition de la communauté des six espèces dominantes de poissons dans cette série de lacs, parmi les plus enrichis au monde en nutriments. La somme des $CPUE_w$ de toutes les espèces augmente avec le statut trophique du lac, déterminé par le dosage de la chlorophylle *a* ($r = 0,45$; $p < 0,009$). Lorsque la $CPUE_w$ totale des poissons est répartie dans les différentes espèces et groupes fonctionnels, seules les $CPUE_w$ de la carpe commune (*Cyprinus carpio*) et des poissons benthonophages augmentent de façon significative avec le statut trophique ($p < 0,03$ et 0,001, respectivement). La proportion des poissons sportifs, principalement des piscivores, dans la $CPUE_w$ totale décline d'environ 50 %, alors que les benthonophages, surtout la carpe commune, s'accroissent d'environ 80 % sur une gamme d'augmentation de la chlorophylle *a* de 10–100 μg·L^{-1}. Il existe une corrélation avec, semble-t-il, un effet négatif entre la $CPUE_w$ de la carpe commune et les $CPUE_w$ du crapet harlequin (*Lepomis macrochirus*) et de la marigane noire (*Pomoxis nigromaculatus*) et un effet positif sur la marigane blanche (*Pomoxis annularis*). Notre étude indique que les espèces non benthonophages n'arrivent pas à exploiter l'augmentation de l'énergie disponible dans les systèmes hypereutrophes ou alors qu'elles sont empêchées par la compétition d'utiliser cette production accrue.

[Traduit par la Rédaction]

Introduction

Eutrophication of fresh water lakes is a worldwide problem. Nutrients enter lakes from agricultural lands, animal feedlots, industry, wastewater treatment plants, and lawn fertilizers (Carpenter et al. 1998; Downing et al. 1999). This rapid increase in nutrients can cause great changes to lake ecosystems. One important resource that can change through eutrophication is the fish community (Persson et al. 1991).

Eutrophication can lead to increased energy supply to fish, but it can also lead to shifts in fish community composition. Trophic state variables such as primary production, chlorophyll *a*, total phosphorus, and total nitrogen have been shown to increase fish production (Hanson and Leggett 1982; Downing et al. 1990; Bachmann et al. 1996). However, as eutrophication increases, some studies have established a systematic loss of piscivorous fish (Bays and Crisman 1983; Persson et al. 1988; Jeppesen et al. 2000), while planktivorous (Yurk and Ney 1989; Bachmann et al. 1996) and benthivorous fish have been observed to increase (Persson et al. 1991; Jeppesen et al. 2000).

A benthivorous fish of particular interest in North America is the common carp (*Cyprinus carpio*). Carp is an invasive, exotic species and has often been associated with

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degradation in water quality and biota. They may increase turbidity within the water column by resuspending sediment (Meijer et al. 1990; Breukelaar et al. 1994; Lougheed et al. 1998), and they can increase nutrient concentrations in lakes directly through excretion (Lamarra 1975) or indirectly through sediment resuspension (Andersson et al. 1978; Breukelaar et al. 1994). Carp may further impact the biota of the ecosystem by uprooting submerged macrophytes while feeding (Crivelli 1983; Ten Winkel and Meulemans 1984), by decreasing benthic invertebrates (Zieba and Szarowska 1987; Tatrai et al. 1994) and zooplankton (Kirk 1991; Lougheed et al. 1998), and by influencing fish species by disrupting nests or through modification of their habitat (Taylor et al. 1984; Harlan et al. 1987).

Because fish possess ecological, commercial, and recreational value, the influence of eutrophication on fish catch in lakes and reservoirs is of great significance to fisheries managers. Despite the notable impacts that carp and other benthivores may have on the fisheries of nutrient-rich lakes, few studies have attempted to analyze trends in fish abundance under highly eutrophic conditions and high abundances of benthivores. Several studies have examined lakes that span a broad range of trophic status (Kautz 1980; Bachmann et al. 1996; Jeppesen et al. 2000) and some have included lakes with benthivores such as bream (*Abramis brama*) and roach (*Rutilus rutilus*) (Persson et al. 1991; Jeppesen et al. 2000), but few have examined a range of lakes in which carp are abundant. Jones and Hoyer (1982) investigated nutrient-rich lakes where carp may have been present, but they only quantified sport fish abundances. Because carp are often implicated in the degradation of eutrophic lake ecosystems, it is important to know how both high nutrient supplies and carp abundances influence fisheries.

Our objectives therefore were to (*i*) examine agriculturally eutrophic lakes to find the best correlates of fish catch, (*ii*) determine how the fish communities change in composition across a gradient of high nutrient concentration, and (*iii*) explore correlations between carp abundance and the abundance and composition of fish communities. Lakes in highly agricultural Iowa, USA, are ideal for this analysis because they are among the worlds most nutrient rich (Arbuckle and Downing 2001), and they frequently have high densities of benthivorous carp.

Methods

The overall approach of our study was to seek correlations between fish catch per unit effort (CPUE) and lake ecosystem characteristics by collecting detailed information of fish CPUE and lake characteristics across 32 eutrophic to hypereutrophic lakes. Fish managers recollect significant management of only a few of these lakes in the 1980s, mostly to eliminate carp. As is typical in this region, none of these management activities altered the species composition for more than a few years. Water samples were collected monthly, May through July 2001, from eight natural and 24 impounded lakes (Fig. 1). Water quality variables that were estimated include chlorophyll *a*, arcsine-transformed percent algal biomass as Cyanobacteria, ammonia measured as the sum of ammonium and un-ionized ammonia, un-ionized ammonia, total nitrogen, total phosphorus, total suspended solids, water transparency, dissolved oxygen, temperature, and specific conductivity. All water samples were collected as integrated samples of the upper mixed zone of each lake. When a thermocline was not present, the entire water column was sampled. Collected water was kept at 4 °C and analyzed within 2 days. Macrophytes occur only sporadically and at very low densities in lakes, so they were not included in our water quality assessments.

Total phosphorus and ammonia were analyzed according to standard methods (American Public Health Association et al. 1998). Total nitrogen was analyzed using second-derivative spectroscopy (Crumpton et al. 1992). Laboratory analysis of chlorophyll *a* was conducted using a Turner Designs TD-700 laboratory fluorometer (Turner Designs Inc., Sunnyvale, California) with acetone and magnesium carbonate extraction (American Public Health Association et al. 1998). Mean estimates of temperature, specific conductivity, and dissolved oxygen were averaged from epilimnetic profiles and were obtained with a YSI 6-Series multiparameter water quality monitor (Yellow Springs Instrument Inc., Yellow Springs, Ohio). Transparency was estimated by Secchi disc depth.

Morphometric variables were collected by Bachmann et al. (1994) and consisted of lake type, lake surface area, mean depth, watershed to lake area ratio, shoreline development index (using equations from Hutchinson 1957), and water residence time.

Fish CPUE estimates were collected by the Iowa Department of Natural Resources between September and October of 2001. Collection methods were standardized to allow comparisons of fish CPUE among lakes. Fyke nets with 12.2-m lead lines and constructed of 0.6 m × 1.2 m frames with seven 0.6-m-diameter hoops enclosed with 1.9-cm bar mesh netting were used to collect fish. These nets were placed randomly within the littoral zone where water measured up to 1.2 m. Nets were set for 24 h before collection and the amount of effort (net nights) varied with lake area and other factors. Three to 15 nets were set per night in lakes <40 ha, 5 to 20 nets were set per night in lakes ranging from 40 to 200 ha, and 7 to 28 nets were set per night in lakes >200 ha. The number of nets set per night in each lake was determined from past experience by local fisheries managers as the number required to obtain a reliable estimate of community composition. Because these lakes are very shallow (average mean depth 2.9 m), fyke nets set at approximately half this depth were assumed to obtain a good representation of fish species found in these lakes.

Fish of stock length (>8 cm for most species) or greater were retained because this is the approximate length that fish reach when mature and the length required for fish to be effectively sampled by gear (Murphy and Willis 1996). Length was measured to the nearest 2 mm, while weight was measured to the nearest 0.5 g. CPUE was determined as an estimate of fish abundance (Murphy and Willis 1996). From CPUE data and fish weights, we estimated fish catch in grams per net per night ($CPUE_w$).

Fish data were analyzed by individual species $CPUE_w$, total $CPUE_w$, and $CPUE_w$ of species grouped by functional categories, i.e., benthivores and sport fish (primarily piscivores). Total $CPUE_w$ consisted of the summed $CPUE_w$ of all species: black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*), bluegill (*Lepomis macrochirus*), chan-

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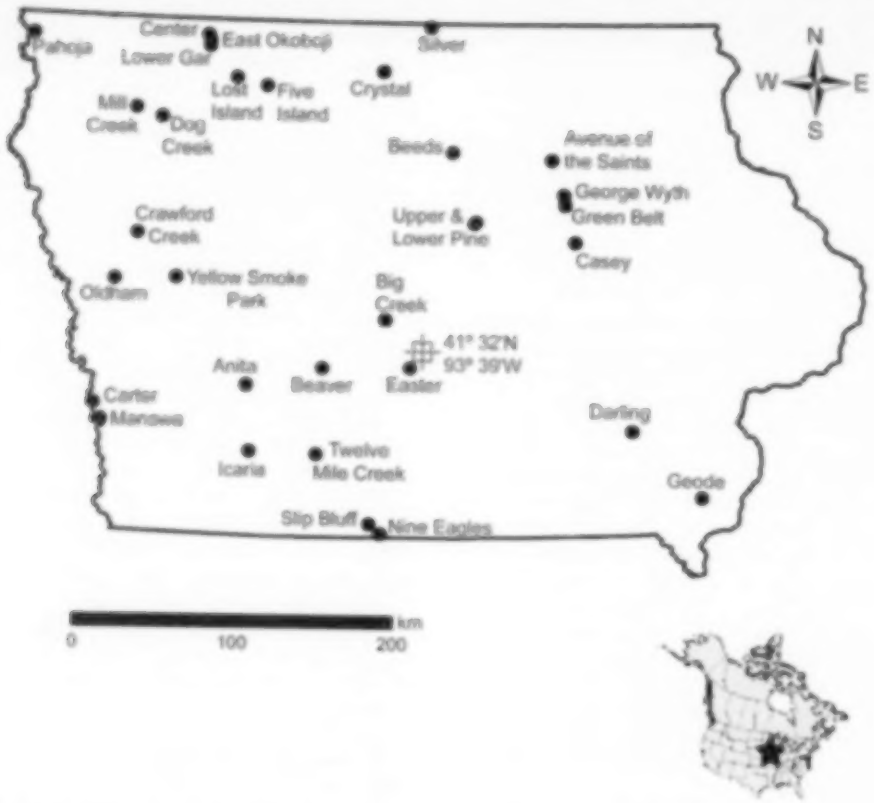
Fig. 1. Location of 32 lakes sampled throughout the state of Iowa, USA. The star on the map of the United States and Canada indicates the position of the state of Iowa on the continent.



nel catfish (*Ictalurus punctatus*), black bullhead (*Ameiurus melas*), common carp, largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), yellow bass (*Morone mississippiensis*), northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), green sunfish (*Lepomis cyanellus*), redear sunfish (*Lepomis microlophus*), freshwater drum (*Aplodinotus grunniens*), and yellow bullhead (*Ameiurus natalis*). Only trends in the first six species were analyzed individually because they were most abundant in these lakes (Harlan et al. 1987), constituted the majority of the fish $CPUE_w$, and could therefore be estimated with confidence. The species caught more sporadically, precluding systematic analysis of trends in catch, were freshwater drum, northern pike, yellow bullhead, green sunfish, redear sunfish, largemouth bass, smallmouth bass, yellow bass, yellow perch, and walleye. These species constituted <13% of the total $CPUE_w$ in most lakes. The sport fish group included black crappie, white crappie, bluegill, and channel catfish. These four species were grouped together because they are important sport fish (Harlan et al. 1987), they are primarily piscivores, and they are not commonly thought to degrade water quality. The benthivore category consisted of common carp and black bullhead. These fish are benthivorous (Harlan et al. 1987) and have been known to degrade water quality through rooting in sediments for food (Keen and Gagliardi 1981; Breukelaar et al. 1994). Although channel catfish are also benthivorous fish, they were not included in this category because they primarily eat fish (Pflieger et al. 1975), they do not root in the sediments for invertebrates, and they are not commonly categorized as a habitat-degrading species.

Because both natural and impounded lakes were combined in the data set, we used bivariate regression analysis to determine whether water quality, morphometric variables, and $CPUE_w$ varied systematically between natural and impounded lakes. Differences in $CPUE_w$ that were found between natural lakes and impoundments were principally attributable to differences in lake morphometry and nutrients. This allowed us to combine both types of lakes and perform bivariate regression analysis between all water quality and morphometric variables and fish $CPUE_w$. The two lake types are distinguished by different symbols in graphical analysis and residuals were examined for homoscedasticity with respect to independent variables and outliers (Gujarati 1995).

Correlation, regression, and variable deletion

Correlations among $CPUE_w$ and independent variables were determined as simple Pearson correlation coefficients (Gujarati 1995). Although correlation analyses were performed using several measures of environmental characteristics, we report the calculated p values without altering them in consideration of multiple comparisons (e.g., Bonferroni correction). There is considerable debate in the statistical literature

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concerning the necessity or meaning of these corrections in exploratory studies such as this (e.g., Perneger 1998; Moran 2003); thus, we follow the advice of Bender and Lange (1999) in labeling our results as exploratory. We also attempted to limit the number of independent variables to those that might logically be expected to influence fish abundance.

Trends in $CPUE_n$ were characterized using ordinary least squares regression analysis. We used ordinary least squares rather than orthogonal or "robust" regression (sensu Draper and Smith 1998), because variances in fyke net estimates of fish catch are very high compared with the variances in independent variables considered here. Results of ordinary least squares and orthogonal regression converge when ratios of variance in dependent to independent variables are large.

Our study lakes are distributed across the landscape, so there is the potential for spatial autocorrelation or spatial patterns altering the interpretation of statistical analyses (Legendre et al. 2002). We did not employ special spatial statistics in this study because spatial variograms indicated no significant spatial structure in the $CPUE_n$ estimates. Indeed, some lakes with the highest $CPUE_n$ were near lakes with very low $CPUE_n$.

Because the list of independent variables suggested to effect fish yield is extensive, the number of variables was decreased to minimize the number of potential comparisons and seriousness of multicollinearity. A correlation matrix (see Appendix A) was examined to discard variables that were highly correlated ($r > 0.70$) (Gujarati 1995). Water residence time was removed because it was correlated with watershed to lake area ratio ($r = 0.89$), and Secchi transparency and ammonia (as the sum of un-ionized ammonia and ammonium) were both removed because of close correlations with total suspended solids ($r = 0.84$ and 0.75, respectively). As a result, we reduced our number of independent variables from 16 to 13.

All variables were $\log_{10}$ transformed to stabilize the variances, linearize the responses, and normalize the residuals (Draper and Smith 1998). $CPUE_n$ data were $\log_{10}(x + 1)$ transformed to allow zeros to be included in regressions. Using JMP 5.0® (SAS Institute Inc., Cary, North Carolina), bivariate and multiple regression (using stepwise selection) analyses were performed between individual species $CPUE_n$, total $CPUE_n$, and $CPUE_n$ of fish categories (i.e., sport fish, benthivores) and all remaining independent variables.

Species composition

To examine changes in fish composition with eutrophication, we performed simple regression analyses between the $CPUE_n$ of individual species, sport fish, and benthivorous categories and chlorophyll *a*. Chlorophyll *a* was used as an overall measurement of eutrophication because it has been shown to be positively correlated with nutrient concentration (e.g., Jones and Bachmann 1976) and photosynthetic production (e.g., Smith 1979) and provides an index of lake trophic state (e.g., Carlson 1977).

We determined the relative importance of individual species, sport fish, and benthivores in the fish community by examining the relationship between the fraction of total $CPUE_n$ for each and chlorophyll *a* concentration. The percentages were arcsine transformed using $\sin^{-1}(\sqrt{x})$ (where x is the percent composition of fish $CPUE_n$) to prevent the data from being skewed toward 0% or 100% (Quinn and Keough 2002).

Carp influences on catch of other species

Because the fisheries literature suggests that carp can have deleterious effects on other fish species (Taylor et al. 1984; Harlan et al. 1987), bivariate and multiple regression analyses were performed to compare the $CPUE_n$ of individual fish and sport fish with carp $CPUE_n$ in all lakes and in lakes containing carp.

Results

Lakes surveyed were in the most fertile range of nutrients worldwide (e.g., Downing and McCauley 1992). Most independent variables spanned a range of more than an order of magnitude (chlorophyll *a*, un-ionized ammonia, total nitrogen, total phosphorus, total suspended solids, and watershed to lake area ratio) and lake surface area ranged over two orders of magnitude (Appendix B). Because lake mean depth averaged 2.9 m and total phosphorus ranged from 27 to 300 $\mu g \cdot L^{-1}$, these lakes can be classified as shallow, nutrient-rich lakes.

Predictors of fish $CPUE_n$

The ranges of $CPUE_n$ for all fish and fish categories are given in Appendix C. As others have found, our study revealed a significant, positive correlation between fish catch and lake trophic status as measured by chlorophyll *a* (Fig. 2). Chlorophyll *a* was a strong correlate ($p < 0.01$) of total fish $CPUE_n$ in bivariate analyses ($r = 0.45$) (Table 1). Other independent variables correlating with the $CPUE_n$ of the six major fish species included lake surface area and mean depth ($r = 0.50$ and -0.37, respectively) (Table 1). There were no multivariate relationships of total $CPUE_n$ and environmental characteristics that accounted for significantly more variation than the bivariate regressions.

The best correlates of individual species and fish group $CPUE_n$ varied with a diversity of lake characteristics. Bluegill $CPUE_n$ tended to be highest in small lakes, while the largest $CPUE_n$ of carp was found in large lakes ($r = -0.39$ and 0.53, respectively). Black bullhead and the benthivore group both yielded higher $CPUE_n$ in shallow lakes ($r = -0.40$ and -0.58, respectively). Black crappie and channel catfish $CPUE_n$ increased and decreased, respectively, with specific conductivity ($r = 0.40$ and -0.39, respectively), while the $CPUE_n$ of white crappie increased with total suspended solids ($r = 0.37$) and the sport fish group $CPUE_n$ decreased with dissolved oxygen ($r = -0.37$) (Table 2).

Stepwise analyses to determine the best predictors of $CPUE_n$ for each fish species and fish category yielded results similar to those found in bivariate analyses for black crappie, white crappie, and channel catfish, while the best predictor for black bullhead switched from mean depth to specific conductivity ($r = 0.37$) (Table 2). Carp and benthivore $CPUE_n$ were the only fish for which the stepwise analyses yielded significant multiple regressions. Carp $CPUE_n$ was highest in large, shallow, highly conductive lakes, while benthivore $CPUE_n$ was highest in large, shallow lakes with high chlorophyll *a* concentrations (Table 3).

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Fig. 2. Relationship between total fish catch per unit effort by weight ($CPUE_w$) (g·net^{-1}·night^{-1}) and chlorophyll *a* (μg·L^{-1}) (r = 0.45, $p < 0.01$). "Total" means the summed catch of all species caught in fyke nets. Solid circles, impounded lakes; open circles, natural lakes.

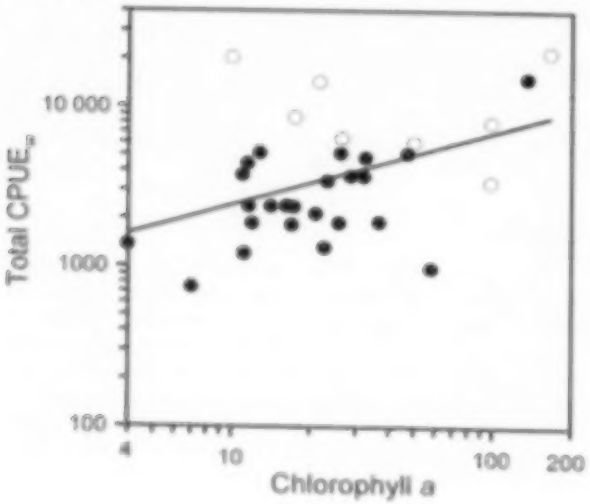

Table 1. Regression equations of variables correlated with the $\log_{10}$ of total fish catch per unit effort by weight ($CPUE_w$) (g·net^{-1}·night^{-1}).

Bivariate regression	n	r	p
2.93 + 0.31 ($\log_{10}$ SA)	32	0.50	0.003
2.93 + 0.46 ($\log_{10}$ Chl *a*)	32	0.45	0.009
3.89 – 0.78 ($\log_{10}Z$)	30	–0.37	0.043

Note: SA, lake surface area (ha); Chl *a*, chlorophyll *a* concentration (μg·L^{-1}); Z, mean depth (m).

Variables related to a gradient of eutrophication were seldom correlated with fish $CPUE_w$. In fact, carp, white crappie, and benthivores were the only fish groups that responded positively to indices of lake trophic status. Chlorophyll *a* and total nitrogen were positively correlated with carp $CPUE_w$, while total suspended solids correlated positively with the $CPUE_w$ of white crappie (r = 0.38, 0.35, and 0.37, respectively) (Table 2). Carp were also partially responsible for the positive correlation between total phosphorus and benthivorous fish (r = 0.40) because carp made up an average 70% of the $CPUE_w$ for this group.

Species composition

Benthivore and carp $CPUE_w$ increased significantly across a gradient of chlorophyll *a* ($p < 0.001$ and 0.03, respectively) (Fig. 3), while no other species or groups of fish were significantly related to lake trophic status. These results changed when we examined the relative importance of individual species and functional categories, expressed as a percentage of total $CPUE_w$ across a chlorophyll *a* gradient. Benthivore $CPUE_w$, expressed as a fraction of the total $CPUE_w$ increased significantly with chlorophyll *a*, while percent bluegill and sport fish $CPUE_w$ decreased significantly ($p < 0.05$, 0.01, and 0.03, respectively) (Fig. 4).

Carp influences on catch of other species

Because carp $CPUE_w$ became dominant as total fish $CPUE_w$ increased (Fig. 5), there may be a possibility that carp can have deleterious impacts on other fish species. Bivariate analyses revealed a significant increase in white crappie $CPUE_w$ and a significant decrease in bluegill $CPUE_w$ with carp $CPUE_w$ ($p < 0.03$ and 0.05, respectively) (Fig. 6). Stepwise selection analyses indicated that carp $CPUE_w$ was not a strong predictor of any individual fish $CPUE_w$.

Because deleterious effects of carp would be expected to be most apparent at high carp standing stock, we also analyzed the relationships between carp and other species in the lakes containing carp. Results of regression analyses from lakes with carp indicated that only black crappie decreased significantly ($p < 0.03$) (Fig. 6). Further, stepwise selection analyses found that carp explained a significant additional amount of variance in only the $CPUE_w$ of black crappie (R^2 = 0.59, $p > 0.005$) (Table 3).

Discussion

Overall, our study showed that total fish $CPUE_w$ increased with lake trophic status, but with weaker correlations and with fewer trophic status variables showing significant trends than other studies. Chlorophyll *a* was the water quality variable that was best correlated with the total $CPUE_w$ (r = 0.45). This result is similar to the results of Oglesby (1977), Bays and Crisman (1983), and Bachmann et al. (1996). They have found total fish catch to increase systematically with chlorophyll *a* (r = 0.92, 0.67, and 0.52, respectively) in lakes with chlorophyll *a* ranges similar to ours (1 to >130 μg·L^{-1}). Increased fish catch with chlorophyll *a* is expected because algal primary production fuels the base of the trophic pyramid in these nearly macrophyte-free lakes. This production can benefit all trophic levels above it, including fish. Surprisingly, other variables related to lake trophic status, such as total phosphorus and total nitrogen, were not correlated with total fish $CPUE_w$. This result differs from those of Hanson and Leggett (1982), Downing et al. (1990), and Bachmann et al. (1996), who found that these variables were positively correlated with fish catch, biomass, or production.

The weak correlation with chlorophyll *a* and lack of correlations with nutrient concentrations may result from several factors. The most likely explanation is due to decoupling of high concentrations of the nutrients nitrogen and phosphorus from production in these lakes receiving high inputs from agricultural land. Because nutrients are so abundant, nitrogen and phosphorus may no longer be primary production limiting resources (Arbuckle and Downing 2001). Instead, suspended solids may lead to light limitation in some lakes, while nutrients may limit phytoplankton in others. Studies of both algal biomass (Watson et al. 1992) and fish catch (Jeppesen et al. 1997) have suggested production approaching an asymptote in nutrient-rich systems. In place of nitrogen and phosphorus as the limiting resources in these lakes, other variables such as lake surface area and mean depth could become stronger correlates of total fish $CPUE_w$. This

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Table 2. Significant correlation coefficients (r) between independent variables and catch per unit effort by weight ($CPUE_w$) (g·net^{-1}·night^{-1}) of individual and grouped fish species.

	BLG	BLC	WHC	CARP	BBHD	CCF	SPORT	BENTH
LType	–0.44			+0.51	+0.68		–0.42	+0.61
$\bar{Z}$				–0.46	–0.40			–0.58
SA	–0.39			+0.53				+0.47
Cond		+0.40		+0.48	+0.37	–0.39		+0.37
DO							–0.37	
Chl *a*				+0.39				+0.57
TN				+0.35				
TP								+0.40
TSS			+0.37					

Note: LType, lake type; $\bar{Z}$, mean depth (m); SA, lake surface area (ha); Cond, specific conductivity (mS·cm^{-1}); DO, dissolved oxygen concentration (mg·L^{-1}); Chl *a*, chlorophyll *a* concentration (μg·L^{-1}); TN, total nitrogen concentration (mg·L^{-1} as N); TP, total phosphorus concentration (μg·L^{-1} as P); TSS, total suspended solids concentration (mg·L^{-1}); BLG, bluegill; BLC, black crappie; WHC, white crappie; CARP, common carp; BBHD, black bullhead; CCF, channel catfish; SPORT, sport fish group: summed $CPUE_w$ of BLG, BLC, WHC, and CCF; BENTH, benthivore group: summed $CPUE_w$ of CARP and BBHD. The slope of the regression line is indicated as "+" for positive and "-" for negative. Only significant correlations ($p < 0.05$) are listed. Independent variables showing no correlation with fish $CPUE_w$ were temperature, un-ionized ammonia, arcsine-transformed percent algal biomass made up of Cyanobacteria, watershed to lake area ratio, and shoreline development index (Murphy and Willis 1996).

Table 3. Regression models showing the best predictors for species-specific and species group catch per unit effort by weight ($CPUE_w$) (g·net^{-1}·night^{-1}) and regression models obtained when common carp $CPUE_w$ was added to the list of independent variables in lakes with high carp $CPUE_w$ (>180 g·net^{-1}·night^{-1}).

Multiple regression	n	R^2	p
CARP = 2.75 + 3.76(Cond) – 3.08($\bar{Z}$) + 1.15(SA)	30	0.54	<0.001
BENTH = 2.89 + 3.17(Cond) – 2.48($\bar{Z}$) + 1.47(Chl *a*)	30	0.61	<0.0001
CARP included as independent variable: BLC = 9.01 – 1.86(TP) – 0.86(CARP)	15	0.59	<0.005

Note: Stepwise selection of independent variables was used to obtain the models. Cond, specific conductivity (mS·cm^{-1}); $\bar{Z}$, mean depth (m); SA, lake surface area (ha); Chl *a*, chlorophyll *a* concentration (μg·L^{-1}); TP, total phosphorus concentration (μg·L^{-1} as P); CARP, common carp; BLC, black crappie; BENTH, benthivore group: summed $CPUE_w$ of BBHD (black bullhead) and CARP. Only statistically significant multiple regressions ($p < 0.05$) are shown.

implies that although we see an increase in total fish $CPUE_w$ with lake trophic status as measured by chlorophyll *a*, increases in fish $CPUE_w$ may not be as simple as others have found. This may be especially true in agriculturally enriched hypereutrophic lakes where production may be limited by suspended solids, nitrogen, or phosphorus, depending on the configuration of the lake and its watershed.

Other potential reasons for lack of correlations between total fish $CPUE_w$ and nutrients could be due to the near lack of macrophytes in these lakes or to low statistical power resulting from well-known high within-lake error in estimation of fish catch. Macrophytes add complexity to the lake ecosystem and allow multiple pathways for nutrients to increase habitat and food for fish (Scheffer 1998). Spatial distributions of fish or errors introduced during collection can increase variability of catch data (Murphy and Willis 1996) and cause low statistical power (Draper and Smith 1998) for the detection of statistical trends.

Correlations of total fish $CPUE_w$ with other variables considered to be important to fish were infrequent. Water quality and morphometric variables such as water temperature, dissolved oxygen concentration, Cyanobacteria, un-ionized ammonia, and the shoreline development index may influence fish (Alabaster and Lloyd 1982; Guy and Willis 1995; Paerl et al. 2001), but we did not observe significant correlations between total fish $CPUE_w$ and these variables. This is likely due to shifts in the fish community toward species tolerant of poor water quality as ecosystems became enriched.

Taxon-specific $CPUE_w$ and community composition

The only fish that appeared to capture increased energy from increased lake trophic status were carp and the benthivore group. The $CPUE_w$ of carp and benthivores (consisting of an average of 70% carp) were both strongly correlated with chlorophyll *a*. Carp $CPUE_w$ was also correlated with total nitrogen, while benthivore group $CPUE_w$ was correlated with total phosphorus. White crappie catch may also increase somewhat with lake trophic status, as indicated by the increase in $CPUE_w$ with total suspended solids. These results suggest that only a few taxa respond positively to eutrophication in these lakes and that catches of species that are more economically and socially desirable (i.e., bluegill, black crappie, and channel catfish) do not increase with hypereutrophication.

As eutrophication, measured by chlorophyll *a*, increased in these lakes, a systematic shift in fish species composition from the desirable sport fish (primarily piscivores) to less desirable benthivores occurred. The $CPUE_w$ of carp and other benthivores increased systematically across a chlorophyll *a* gradient, while sport fish $CPUE_w$ showed lit-

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Fig. 3. Variation in community composition (estimated from catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$)) with increasing lake trophic status estimated from chlorophyll *a* ($\mu g \cdot L^{-1}$). Solid lines indicate significant regression slopes ($p < 0.05$), while broken lines indicate nonsignificant relationships ($p > 0.05$). BLC, black crappie; BLG, bluegill; WHC, white crappie; CCF, channel catfish; CARP, common carp; BBHD, black bullhead; SPORT, sport fish group (i.e., sum of BLC, WHC, BLG, and CCF); BENTH, benthivore group (i.e., sum of BBHD and CARP); Total, total fish (i.e., the summed catch of the all species caught by fyke nets in these lakes). Individual data points are not shown to avoid confusion.

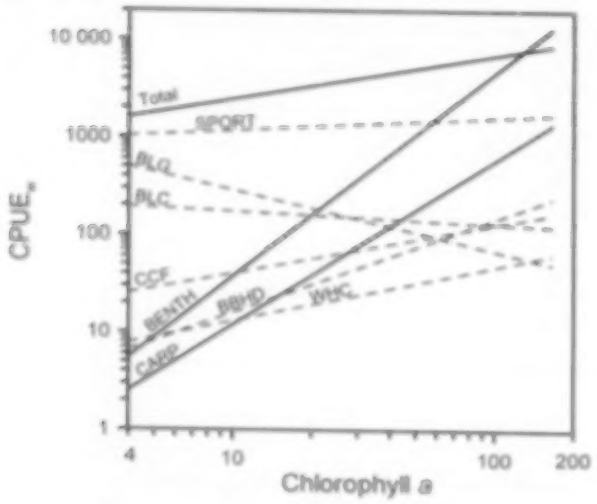


Fig. 4. Variation in relative importance (arcsine-transformed fraction of total fish catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$)) of bluegill (BLG), sport fish (SPORT), and benthivores (BENTH) plotted against chlorophyll *a* ($\mu g \cdot L^{-1}$) ($p < 0.002$, 0.03, and 0.01, respectively). The units on the right *y* axis represent approximate percentages of fish $CPUE_w$ when the units on the left *y* axis are untransformed. Individual data points were not shown to avoid confusion.

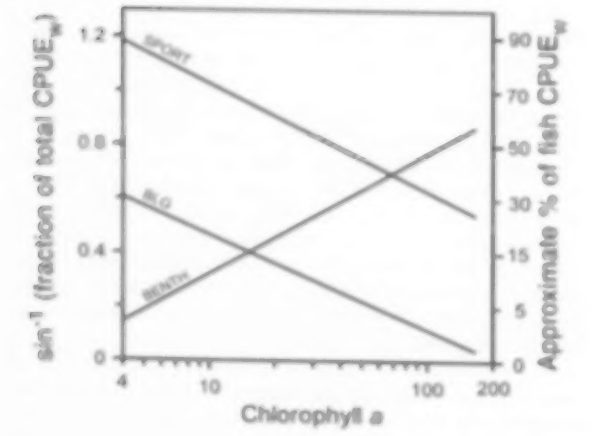
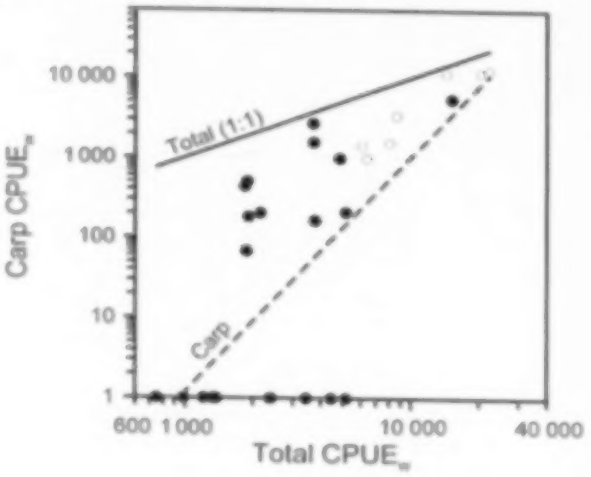


Fig. 5. Relationship between common carp and total fish catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$) showing carp dominating total fish $CPUE_w$ at high biomass. The solid line indicates a 1:1 relationship of total fish $CPUE_w$, while the broken line represents an ordinary least squares regression of the relationship between total fish and carp $CPUE_w$. Solid circles, impounded lakes; open circles, natural lakes.



tle systematic change. Carp and benthivore $CPUE_w$ increased by approximately 100% over a chlorophyll *a* range of 10–100 $\mu g \cdot L^{-1}$. The relative importance (fraction of total $CPUE_w$) of species also showed that benthivore $CPUE_w$ increased by 80% over a range of chlorophyll *a* of 10–100 $\mu g \cdot L^{-1}$. However, the sport fish and bluegill fraction of total biomass decreased by approximately 50% and 80%, respectively, across the same range of chlorophyll *a*. Such a shift from sport fish (primarily piscivores) to benthivores agrees with Persson et al. (1991) who found that benthivores (roach and bream) replaced piscivores and eventually dominated ecosystems over a similar chlorophyll *a* gradient in Europe.

Jones and Hoyer's (1982) results differed from ours in that they found that the yield of sport fish increased systematically across a similar chlorophyll *a* gradient ($r = 0.91$). Our yields of sport fish did not increase systematically with chlorophyll *a*. Detailed analysis of our data indicated that Silver Lake was a strong outlier that was very high in chlorophyll *a* (100 $\mu g \cdot L^{-1}$) but yielded few fish other than black bullhead. If we categorize black bullhead as a sport fish, as done by Jones and Hoyer (1982), we also see a positive correlation with chlorophyll *a* ($r = 0.41$, $p < 0.02$). This regression may reveal a species shift from piscivores to benthivores, however, more than an increase in sport fish with increased lake trophic status. Silver Lake has an extremely high concentration of un-ionized ammonia (415 $\mu g \cdot L^{-1}$), which can be toxic to intolerant fish such as piscivores at concentrations >200 $\mu g \cdot L^{-1}$ (Alabaster and Lloyd 1982). Because black bullheads are more tolerant than piscivores of decreases in water quality, they appear to replace piscivores and make up the entire catch in this lake. Because Jones and Hoyer (1982) did not indicate the fish species yields along the entire trophic gradient, their regres-

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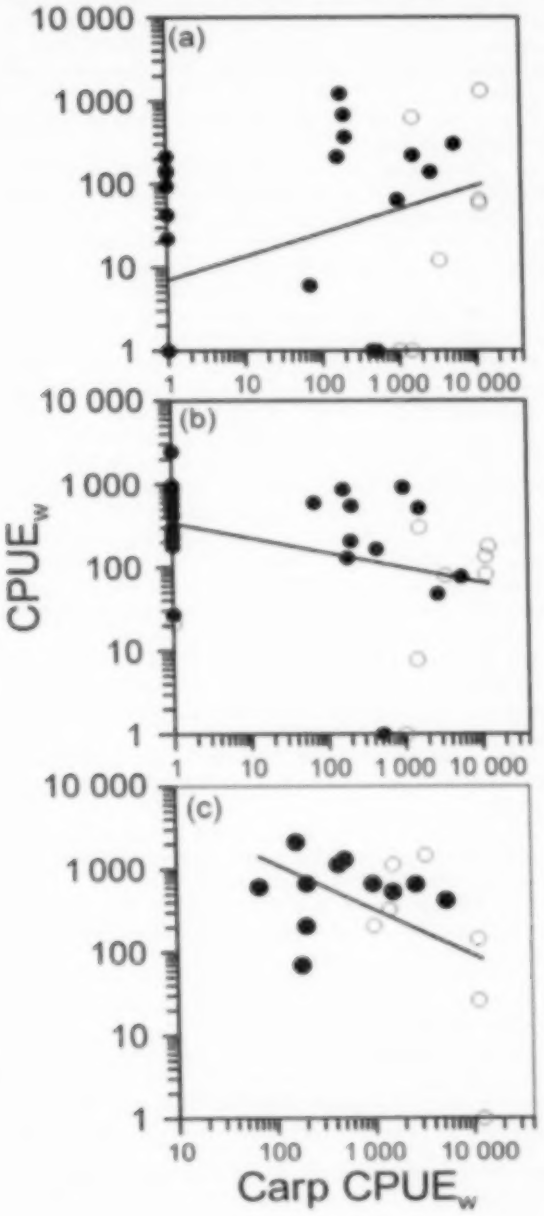
Fig. 6. Relationship between common carp catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$) and the $CPUE_w$ of (*a*) white crappie ($r = 0.40$, $p < 0.03$), (*b*) bluegill ($r = -0.36$, $p < 0.05$), and (*c*) black crappie ($r = -0.49$, $p < 0.03$). White crappie and bluegill figures represent a regression using all lakes, while that of black crappie represents a regression from lakes with carp. Solid circles, impounded lakes; open circles, natural lakes. Note the scale change between bluegill and black crappie figures.



sion may not suggest that the most desirable fish will offer high yields in the most eutrophic lakes. Our data indicate that the only species benefiting substantially from increases in lake trophic status are the benthivores.

There are many possible reasons for this shift from sport fish to benthivores in eutrophic lakes. Sport fish (primarily picivores) depend on clear water because they are principally visual feeders (Bruton 1985). Young-of-the-year piscivores typically rely on zooplankton as a food source, but because large zooplankton are often rare in turbid eutrophic lakes (Jeppesen et al. 2000), food shortages may limit piscivore growth and recruitment. Benthivores, especially carp, are not limited by turbid water because they are tolerant of great levels of turbidity (>200 $g \cdot L^{-1}$; Alabaster and Lloyd 1982). They also may not encounter food shortages because zoobenthos may be less impacted than zooplankton under hypereutrophic conditions (Scheffer 1998). Some sport fish depend on aquatic macrophytes for habitat (Grimm and Backx 1990), whereas macrophytes often decrease with increased eutrophication (Egertson et al. 2004) and carp abundance (Crivelli 1983). Hypereutrophic ecosystems may therefore represent very poor habitat for sport fish.

Carp influences on other species

Carp $CPUE_w$ was strongly correlated with $CPUE_w$ of white crappie and bluegill when analyzed across all lakes and with black crappie $CPUE_w$ when considering only lakes with carp. This may indicate some antagonism between these species or potential competitive exclusion. The positive correlation between white crappie $CPUE_w$ and carp $CPUE_w$ may result from white crappies' good adaptation to turbid, shallow waters (Carlander 1977). On the other hand, bluegills and black crappies, some of the most important sport fishes in the highly eutrophic lakes of the Midwest USA (Harlan et al. 1987), are both intolerant of continuous high turbidity and siltation and grow best in clear water (Pflieger 1975; Harlan et al. 1987).

Although the relationship found between bluegill, black crappie, and carp $CPUE_w$ could simply be chance correlations owing to contrasting habitat requirements, carp may directly impact these fish by interfering with reproduction and growth. Both bluegill and black crappie build nests in shallow waters (<0.5–2 m; Harlan et al. 1987) where carp are typically found (Pflieger 1975). Nests may therefore be in jeopardy of disruption by the benthos-feeding carp. Because white crappie can spawn in deeper waters (1–3 m; Harlan et al. 1987), their nests may be able to escape this disturbance. Carp may also impact bluegill and black crappie by decreasing habitat through uprooting macrophytes (Crivelli 1983), by outcompeting young-of-the-year fish by decreasing zooplankton and aquatic insects (Tatrai et al. 1994; Lougheed et al. 1998), and by resuspending sediment (Breukelaar et al. 1994), limiting the ability of bluegill and black crappie to see prey. It is therefore plausible that carp may experience differential success in hypereutrophic ecosystems not only because of their resistance to poor water quality conditions but also because they may competitively exclude other species.

In conclusion, counter to the results of other studies, we found that benthivorous fish were the principal beneficiaries of increased eutrophication in these agriculturally enriched lakes. Benthivorous carp become so dominant that their responses to lake conditions determine the trends of total fish $CPUE_w$. Our study indicates that, with the tremendous increase in eutrophication and carp abundance, species other than benthivores seem unable to exploit the increased energy

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available in hypereutrophic systems. Thus, fisheries responses to hypereutrophication are characterized by the shunting of resources to benthivorous fish, with little net gain in biomass for sport fish (primarily piscivores), in these very fertile lakes.

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Appendices appear on the following pages.

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Appendix A

Table A1. Correlation matrix of all independent variables.

	°C	Cond	DO	Chl *a*	NH3	TN	TP	TSS	BG	W:L	$\bar{Z}$	SA	SDI	RT	NH4	Secchi
°C	—	–0.20	0.39	0.11	0.63	–0.39	–0.10	0.34	0.10	–0.35	–0.18	0.10	–0.20	0.10	0.34	–0.40
Cond	–0.20	—	0.07	0.12	–0.10	0.22	0.00	–0.15	0.23	0.20	–0.27	0.11	0.00	0.00	–0.25	0.25
DO	0.39	0.10	—	0.14	0.41	–0.28	–0.18	0.04	0.16	–0.27	–0.10	0.12	–0.20	0.22	0.14	–0.14
Chl *a*	0.11	0.12	0.14	—	0.44	0.32	0.55	0.49	0.32	0.00	–0.37	0.44	–0.30	–0.10	0.28	–0.64
NH3	0.63	–0.10	0.41	0.44	—	–0.15	0.31	0.52	0.45	–0.33	–0.30	0.20	–0.30	0.17	0.55	–0.52
TN	–0.40	0.22	–0.28	0.32	–0.20	—	0.50	0.00	–0.10	0.55	0.06	0.16	0.10	–0.50	–0.10	0.00
TP	0.00	0.00	–0.18	0.55	0.31	0.50	—	0.62	0.29	0.20	–0.17	0.30	–0.30	–0.30	0.62	–0.64
TSS	0.34	–0.20	0.04	0.49	0.52	0.00	0.62	—	0.19	–0.24	–0.54	0.33	–0.40	0.00	0.75	–0.84
BG	0.10	0.23	0.16	0.32	0.45	–0.10	0.29	0.19	—	–0.19	–0.12	0.25	–0.30	0.26	0.21	–0.10
W:L	–0.40	0.20	–0.27	0.00	–0.30	0.55	0.20	–0.24	–0.19	—	0.19	–0.30	0.23	–0.90	–0.20	0.18
$\bar{Z}$	–0.20	–0.30	–0.10	–0.37	–0.30	0.06	–0.17	–0.54	–0.12	0.19	—	0.00	0.59	0.10	–0.10	0.44
SA	0.10	0.11	0.12	0.44	0.20	0.16	0.30	0.33	0.25	–0.34	–0.10	—	0.14	0.35	0.24	–0.29
SDI	–0.20	0.00	–0.15	–0.29	–0.30	0.07	–0.27	–0.39	–0.30	0.23	0.59	0.14	—	0.00	–0.13	0.31
RT	0.10	0.00	0.22	–0.12	0.17	–0.48	–0.27	0.01	0.26	–0.89	0.07	0.35	0.00	—	0.12	0.08
NH4	0.34	–0.30	0.14	0.28	0.55	–0.10	0.62	0.75	0.21	–0.20	–0.10	0.24	–0.10	0.12	—	–0.70
Secchi	–0.40	0.25	–0.14	–0.64	–0.50	0.00	–0.64	–0.84	–0.10	0.18	0.44	–0.30	0.31	0.10	–0.70	—

Note: Values are correlation coefficients (r) and a dash indicates the correlation of a variable with itself. °C, mean summer temperature; Cond, specific conductivity (mS·cm^{-1}); DO, dissolved oxygen concentration (mg·L^{-1}); Chl *a*, chlorophyll *a* concentration (μg·L^{-1}); NH3, un-ionized ammonia concentration (μg·L^{-1} as N); TN, total nitrogen concentration (mg·L^{-1} as N); TP, total phosphorus concentration (μg·L^{-1} as P); TSS, total suspended solids concentration (mg·L^{-1}); BG, arcsine-transformed percentage of algae biomass made up of Cyanobacteria; W:L, ratio of watershed to lake area; $\bar{Z}$, mean depth (m); SA, lake surface area (ha); SDI, shoreline development index (Murphy and Willis 1996); RT, water residence time (years); NH4, ammonia (as the sum of un-ionized ammonia and ammonium, $NH_3 + NH_4$); Secchi, Secchi disc transparency (m).

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Appendix B

Table B1. Lake characteristics of 32 lakes surveyed during the summer of 2001.

Lake	LType	°C	Cond	DO	Chl *a*	NH3	TN	TP	TSS	BG	W:L	$\bar{Z}$	SA	SDI
Avenue of the Saints Lake	I	23.2	0.2	6.3	47	67	1.8	115.8	17.4	0.8	na	na	12.1	na
Beaver Lake	I	24.6	0.3	7.8	11.6	36.6	1.9	67	5.4	–0.1	29.5	2.9	14.1	2.5
Beeds Lake	I	19.1	0.5	8.2	32.4	7	13.8	164.4	7.2	–1.1	187.2	2.6	41	2.1
Big Creek Lake	I	21.4	0.4	7.1	11.9	16.7	9.3	88.9	5.9	–0.4	55	5.4	357.4	5.1
Carter Lake	N	24.2	0.6	8.3	98.5	49.0	2	181.2	21.4	1.7	36.8	2.5	128	2.7
Casey Lake	I	22.4	0.3	5.9	14.1	85.1	1.9	123.3	6.4	1.2	13.6	3.1	22	2.4
Center Lake	N	22.4	0.6	10.2	50	26.6	2	113.3	6.7	1.7	2.7	2.9	110	2
Crawford Creek	I	22.1	0.5	na	12.8	35.1	1	43	10.7	0.1	38.3	3.4	25	2.3
Crystal Lake	N	23.8	0.3	9	165	89	3.1	300.6	40	0.9	6.8	1.4	108.6	1.2
Dog Creek Lake	I	20.6	0.6	5.3	17.3	30.1	5.2	154.4	11.6	0.7	105.5	3	11	2
East Okoboji Lake	N	21.8	0.5	8.8	9.9	16.9	1.1	59.4	3.9	1.1	6.7	3.2	743	2.8
Easter Lake	I	25.1	0.5	12.4	26.1	209.9	1.3	87.5	13.5	–0.1	51.7	3.3	70	3.6
Five Island Lake	N	22.8	0.4	8.2	17.4	50.9	2.7	59.2	16.5	0	8.9	1.4	384.9	3.3
George Wyth Lake	I	24.7	0.4	6.9	11	31.3	1	27.5	10.1	0.1	12.5	2.7	21	1.6
Green Belt Lake	I	24.9	0.5	7.2	11.5	31	0.7	26.5	5.8	2.1	na	na	8.9	na
Lake Anita	I	23.3	0.2	8.2	58	49.4	1.4	51.1	13	–0.2	na	3.7	74	4.1
Lake Darling	I	24.9	0.2	7.1	20.9	58.9	5.2	252.4	57.2	0.1	40.7	2.7	121	3.4
Lake Geode	I	23.8	0.3	11.5	16.2	67.6	4.4	71	4.2	0.9	52.2	7.2	76.5	3.1
Lake Icaria	I	23.1	0.2	6.2	23.2	32.1	2.8	67	14.9	–0.7	25	3.4	270.9	4.7
Lake Manawa	I	24.3	0.5	10.7	36.6	94.2	1.2	89.5	17.4	0	3.5	1.9	289.1	2.1
Lake Pahoja	I	21.1	0.8	8.8	17	47.8	6.9	87.4	7.4	1.2	62.5	3.2	25.6	2.9
Lower Gar Lake	N	23.8	0.5	9.3	21.5	40.1	1.2	91.3	25.8	0.3	47	1.1	97.9	1.8
Lost Island Lake	N	22.7	0.4	10.7	26.4	64	2.2	110	19.7	0.9	4	3.1	464.3	1.5
Lower Pine Lake	I	24.2	0.3	6.9	32	72	7.8	104	11.9	–1.1	16.9	2	20	1.5
Mill Creek (Lake)	I	22.6	0.5	6.8	25.7	35	2.3	59.9	7.9	0.6	123.3	1.5	12	1.7
Nine Eagles Lake	I	22.6	0.2	8.6	7	16.1	0.6	37.4	6.8	–0.3	19	4.2	25.4	2.3
Oldham Lake	I	21.6	0.4	11.5	22.6	31.9	1.2	57.9	6.8	–0.3	46.5	3	6	3.3
Silver Lake	N	24.3	0.2	13.3	98	414.7	1.6	119.9	33.8	1.3	8.1	1.4	128	1
Slip Bluff Lake	I	21.9	0.2	7.4	4	17.6	0.9	94.2	15.4	–0.6	15.5	3.8	6	2.3
Twelve Mile Creek Lake	I	22.7	0.3	8.1	135.4	30.2	2.6	59.6	7.5	0	21.3	4.6	267.3	3.9
Upper Pine Lake	I	22.4	0.4	9.3	28.5	17.7	11.4	67.9	6.2	0.1	120.1	2.2	28	2.2
Yellow Smoke Park Lake	I	22.5	0.4	6.4	11.1	22.2	1.3	46.7	5.3	–0.7	50.5	3.4	11.7	3.6

Note: All concentrations are the mean summer concentrations from the upper mixed zone. LType, lake type: I indicates an impounded lake, N indicates a natural lake; °C, mean summer temperature; Cond, specific conductivity ($mS \cdot cm^{-1}$); DO, dissolved oxygen concentration ($mg \cdot L^{-1}$); Chl *a*, chlorophyll *a* concentration ($\mu g \cdot L^{-1}$); NH3, un-ionized ammonia concentration ($\mu g \cdot L^{-1}$ as N); TN, total nitrogen concentration ($mg \cdot L^{-1}$ as N); TP, total phosphorus concentration ($\mu g \cdot L^{-1}$ as P); TSS, total suspended solids concentration ($mg \cdot L^{-1}$); BG, arcsine-transformed percentage of algae biomass made up of Cyanobacteria; W:L, ratio of watershed to lake area; $\bar{Z}$, mean depth (m); SA, lake surface area (ha); SDI, shoreline development index (Murphy and Willis 1996); na, missing datum.

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Appendix C

Table C1. Catch per unit effort by weight ($CPUE_w$) (g·net^{-1}·night^{-1}) from 32 lakes surveyed in the fall of 2001.

Lake	LType	Nets	BBHD	CARP	BLC	WHC	BLG	CCF	SPORT	BENTH	Total
Avenue of the Saints Lake	I	6	62	0	1216	0	701	2987	4904	62	5 150
Beaver Lake	I	8	169	0	282	0	438	1497	2217	169	2 390
Beeds Lake	I	6	1314	980	666	63	912	799	2440	2 294	4 834
Big Creek Lake	I	24	0	68	610	5	594	0	1209	68	1 868
Carter Lake	N	16	743	1 573	1140	631	303	3442	5515	2 315	8 035
Casey Lake	I	6	0	0	696	94	855	671	2315	0	2 392
Center Lake	N	20	4272	1 424	330	0	7	0	337	5 696	6 033
Crawford Creek	I	6	0	0	1442	145	2465	1012	5063	0	5 162
Crystal Lake	N	6	131	12 355	0	1333	178	7699	9210	12 485	22 131
Dog Creek (Lake)	I	10	1567	0	530	0	248	0	778	1 567	2 373
East Okoboji Lake	N	14	7559	11 391	25	57	81	0	163	18 950	20 333
Emter Lake	I	16	57	207	666	367	547	1678	3258	264	5 153
Five Island Lake	N	15	343	3 371	1470	11	79	0	1560	3 714	8 587
George Wyth Lake	I	6	157	164	2111	210	864	227	3412	320	3 755
Green Belt Lake	I	5	0	0	81	0	970	3383	4434	0	4 434
Lake Anita	I	12	77	0	289	21	418	54	782	77	983
Lake Darling	I	12	0	202	206	686	205	83	1180	202	2 149
Lake Geode	I	8	0	0	35	0	296	1152	1482	0	2 400
Lake Icaria	I	9	62	0	0	136	26	1931	2093	62	3 434
Lake Manawa	I	16	0	181	69	1232	129	48	1478	181	1 907
Lake Pahoja	I	18	22	435	1133	0	164	0	1297	457	1 831
Lost Island Lake	N	10	3105	996	207	0	0	0	207	4 101	6 373
Lower Gar Lake	N	10	1255	11 381	144	63	135	0	341	12 636	14 311
Lower Pine Lake	I	6	0	2 683	659	138	47	157	1001	2 683	3 683
Mill Creek (Lake)	I	10	69	506	1307	0	0	0	1307	574	1 881
Nine Eagles Lake	I	9	0	0	4	42	222	186	455	0	746
Oldham Lake	I	5	111	0	588	0	565	0	1153	111	1 323
Silver Lake	N	6	2015	0	0	0	20	0	20	2 015	3 416
Slip Bluff Lake	I	9	0	0	34	212	823	304	1373	0	1 374
Twelve Mile Creek Lake	I	9	0	5 449	419	301	76	7578	8373	5 449	15 173
Upper Pine Lake	I	6	0	1 568	535	219	512	0	1265	1 568	3 705
Yellow Smoke Park Lake	I	6	72	0	0	0	179	882	1061	72	1 208

Note: LType, lake type: I indicates an impounded lake, N indicates a natural lake; Nets, effort in net-nights; BBHD, black bullhead; CARP, common carp; BLC, black crappie; WHC, white crappie; BLG, bluegill; CCF, channel catfish; SPORT, sport fish group: summed $CPUE_w$ of BLC, WHC, BLG, and CCF; BENTH, benthivore group: summed $CPUE_w$ of BBHD and CARP; Total, summed $CPUE_w$ of all species caught.

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Oxygen and carbon dioxide transport during sustained exercise in diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*)

Nicholas J. Bernier, Colin J. Brauner, John W. Heath, and David J. Randall

Abstract: To better understand the respiratory physiology of triploid fish, we conducted an analysis of O_2 and CO_2 transport in diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*) swimming at 0.4 body lengths (BL)·s^{-1}, at 2.0 BL·s^{-1}, and at the critical swimming velocity (Ucrit). While O_2 consumption rates (MO_2), MO_2 max, and Ucrit did not differ between ploidies, triploids had a smaller increase in MO_2 over the course of the swimming trial and lower arterial O_2 content (C_aO_2) values than diploids. Relative to diploids, triploids swimming at Ucrit had a reduced Hb–O_2 saturation, lower red blood cell (RBC) pH, but similar O_2 partial pressures (P_aO_2) and methemoglobin values. Overall, triploids and diploids did not differ in C_aCO_2, P_aCO_2, arterial pH, or lactate at any of the swimming speeds. Taken together, triploidy does not appear to impair CO_2 transport or acid–base balance during sustained exercise in chinook salmon. In contrast, our results show that triploids have a smaller O_2 carrying capacity than diploids. While triploids may be able to compensate for their reduced aerobic capacity under the current exercise regime, we suggest that the effects of triploidy on O_2 transport may contribute to the inferior performance of triploid salmon when reared under suboptimal conditions.

Résumé : Afin de mieux comprendre la physiologie respiratoire des poissons triploïdes, nous avons analysé le transport d'O_2 et de CO_2 chez des saumons quinnat (*Oncorhinchus tshawytscha*) diploïdes et triploïdes qui nagent à une vitesse égale à 0,4 leur longueur corporelle (BL)·s^{-1}, à 2,0 BL·s^{-1} et à la vitesse critique de nage (Ucrit). Bien que les taux de consommation d'O_2 (MO_2), MO_2 max et Ucrit ne varient pas entre les deux groupes, les poissons triploïdes subissent une augmentation plus faible de MO_2 et un contenu artériel d'O_2 (C_aO_2) moins élevé que les diploïdes au cours des essais de nage. Par comparaison avec les poissons diploïdes, les triploïdes nageant à Ucrit ont une saturation réduite d'Hb–O_2 et un pH des érythrocytes (RBC) plus bas, mais des pressions partielles d'O_2 (P_aO_2) et des concentrations de méthémoglobine semblables. À toutes les vitesses de nage, les deux groupes n'affichent généralement pas de différences de C_aCO_2, de P_aCO_2, de pH artériel, ni de lactate. Dans l'ensemble, la triploïdie ne semble pas détériorer le transport de CO_2, ni l'équilibre acide–base durant l'exercice soutenu chez le saumon quinnat. En revanche, les poissons triploïdes ont une une capacité de transport de l'O_2 plus faible que les diploïdes. Bien que les poissons puissent compenser pour leur capacité aérobie réduite dans le programme d'exercice actuel, nous pensons que les effets de la triploïdie sur le transport d'O_2 peut contribuer à la performance inférieure des saumons triploïdes élevés dans des conditions suboptimales.

[Traduit par la Rédaction]

Introduction

Developed as a technique to control sexual development in fish in the late 1970s, triploidy can be induced to effectively produce sterile salmonids (Donaldson and Hunter 1982; Thorgaard 1983). In addition to the economic advantages of chromosome set manipulation for maintaining the flesh quality of immature fish, the sterility of triploids may offer an effective means of reducing the genetic impact of cultured fish on wild populations. Aside from having larger but fewer cells and impaired gametogenesis, triploids are remarkably similar to diploids at the whole-animal level (see Benfey 1999 for review). However, despite the similarities between triploids and diploids and their potential advantages in culture, the production of triploid fish has not gained acceptance as a standard practice in the salmonid aquaculture industry (Withler et al. 1998; Benfey 2001). In general, the performance of triploids is inferior to diploids when reared under suboptimal environmental conditions, and the cause for this physiological difference is not understood (Benfey 1999).

Although the aerobic (Small and Randall 1989; Stillwell and Benfey 1996, 1997) and anaerobic (Hyndman et al. 2003*a*) capacities of diploid and triploid salmonids appear to be similar when assessed at cool temperatures, several studies have shown that triploids have reduced survival rates

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when reared or exercised at elevated temperatures (Ojolick et al. 1995; Altimiras et al. 2002; Hyndman et al. 2003*b*). Therefore, while subtle physiological differences between diploids and triploids may be without consequence when metabolic conditions are favourable, they may compromise the physiological performance of triploids when O_2 availability is low and energetic demands are high. Whether these physiological differences are due to a reduction in the O_2 carrying capacity of triploids is not clear. While some studies have found that triploid salmonids have a lower blood hemoglobin (Hb) concentration than diploids (Benfey and Sutterlin 1984*a*; Small and Randall 1989; Sadler et al. 2000), others have observed no difference (Stillwell and Benfey 1996; Benfey and Biron 2000; Hyndman et al. 2003*b*). Similarly, although Graham et al. (1985) found that the amount of O_2 carried by a given amount of Hb is lower in triploids than in diploids, Sadler et al. (2000) found no difference between ploidies in blood O_2 affinity. Still, relative to diploids, there is circumstantial evidence suggesting that the O_2 delivery system of triploid fish may have a reduced capacity. For example, in rainbow trout (*Oncorhynchus mykiss*) infected with bacterial gill disease, triploids experience higher mortality rates than diploids when exposed to hypoxic conditions (Yamamoto and Iida 1994). Similarly, during exercise at high temperatures, triploid brown trout (*Salmo trutta*) appear to have a reduced factorial metabolic scope (Altimiras et al. 2002), and triploid brook trout (*Salvelinus fontinalis*) take longer than diploids to recover from the metabolic disturbances of exhaustive exercise (Hyndman et al. 2003*b*).

In salmonids, the properties of Hb ensure that O_2 uptake and CO_2 excretion at rest are tightly coupled in the red blood cells (RBCs) (Brauner and Randall 1996, 1998; Randall 1998). In brief, the protons produced during Hb oxygenation are the major source of protons for erythrocytic bicarbonate dehydration (Jensen 1989), an essential step for CO_2 excretion in teleosts (Perry et al. 1982). Therefore, any constraints on O_2 uptake imposed by the larger RBC of triploids also have the potential of interfering with CO_2 excretion and vice versa.

To date, neither the pattern of CO_2 excretion nor the O_2 carrying capacity of exercising triploid fish has been examined. Therefore, as a means of improving our basic understanding of the respiratory physiology of triploid fish, we conducted an analysis of O_2 and CO_2 transport during aerobic swimming and at maximal critical swimming velocity (Ucrit) in diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*).

Materials and methods

Experimental fish

Mixed-sex diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*) were obtained from Yellow Island Aquaculture Ltd. (Campbell River, British Columbia, Canada) and held outdoors at the Department of Fisheries and Oceans (West Vancouver, British Columbia, Canada) in separate 200-L fiberglass tanks for at least 1 month prior to experimentation. Fish were fed to satiation with a commercial salmon food and maintained in 29 ppt flow-through seawater at 9 °C. Triploidy was induced by heat shock (Benfey and Sutterlin 1984*c*), and the ploidy of fish was ascertained using propidium iodide flow cytometry (Allen 1983). Diploid fish had a mean body wet weight of 280.5 ± 9.3 g and mean fork length of 27.8 ± 0.3 cm (N = 11). The mean body wet weight and fork length of the triploid fish was 267.9 ± 8.3 g and 27.4 ± 0.4 cm (N = 9), respectively.

Surgical procedure

Salmon were anaesthetized in a 1:10 000 solution of tricaine methanesulphonate (MS-222) in seawater, buffered with $NaHCO_3$ to pH 7.5, and bubbled with air. The anaesthetized fish were transferred to an operating table, where the gills were continually irrigated with a more dilute solution of buffered and aerated MS-222 (1:30 000). The dorsal aorta was cannulated chronically with polyethylene tubing (Clay Adams PE 50, Becton Dickinson, Sparks, Maryland, USA) using the technique of Soivio et al. (1975). Following surgery, weight, fork length, maximum height, and width were recorded, and the fish were allowed to recover for 24 h in separate flow-through opaque acrylic boxes. The cannulae were filled and flushed with heparanized (10 units·mL^{-1} ammonium heparin; Sigma, Missouri, USA) teleost saline solution. The cannulated fish were transferred to a 39.2-L Brett-type swim tube respirometer (Brett 1964) the night before swimming experiments. During this acclimation period, water velocity in the swim tunnel was maintained at 11 cm·s^{-1} (approximately 0.4 body lengths (BL)·s^{-1}), and an overflow of water from the respirometer prevented build up of metabolic waste products.

Experimental protocol

At the start of each swimming trial, the swim tunnel was sealed and the rate of O_2 depletion was recorded over a 6-min interval for calculation of O_2 consumption rate (MO_2). Once resting MO_2 had been assessed, swimming speed was gradually elevated to 1 BL·s^{-1} over a 10-min period and maintained at this velocity for 30 min. The swimming speed was then gradually increased by 0.5 BL·s^{-1} at 30-min intervals until the fish could no longer maintain a given velocity. Thirty minutes is sufficient time for blood–gas and acid–base parameters to stabilize following a change in water velocity (Kiceniuk and Jones 1977; Thomas et al. 1987). MO_2 was determined at each new speed unless the fish fatigued in the first 15-min of the interval. Between estimates of MO_2, the respirometer was flushed with fresh seawater to restore O_2 levels. The maximum swimming speed and time to fatigue were recorded for the calculation of the maximal Ucrit and corrected for the blocking effect of the maximal cross-sectional area of the fish (Beamish 1978).

In each swimming trial, we withdrew three blood samples from the dorsal aorta at set swimming speeds: one 0.5-mL sample at the acclimation velocity and at 2 BL·s^{-1} and one 0.7-mL sample at Ucrit. At each sampling time, we replaced the blood sample by an equivalent volume of heparinized teleost saline. Aliquots of whole blood were taken for measurement of arterial blood O_2 content (C_aO_2), hemoglobin concentration ([Hb]), and red blood cell count (RBCC). In addition, arterial blood partial pressure of O_2 (P_aO_2), red cell pH (pH_i), and methemoglobin concentration ([MetHb]) were assessed at Ucrit. Whole blood was also collected in heparinized capillary tubes. These tubes were sealed, centri-

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Table 1. Hematocrit (Hct), hemoglobin (Hb), red blood cell count (RBCC), mean cellular hemoglobin concentration (MCHC), mean cellular hemoglobin content (MCH), and mean RBC volume (MCV) of diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*) swimming either at 0.4 body lengths (BL)·s^{-1}or 2.0 BL·s^{-1} or at maximal critical swimming velocity (Ucrit).

	Diploid			Triploid		
Parameter	0.4 BL·s^{-1}	2.0 BL·s^{-1}	Ucrit	0.4 BL·s^{-1}	2.0 BL·s^{-1}	Ucrit
Hct (%)	22.8±1.3a	20.0±1.2b	20.4±1.4b	20.7±1.2a	18.9±1.4b	18.7±1.4b
Hb (g·dL^{-1})	9.1±0.6a	7.9±0.5b	8.2±0.6b	8.1±0.5a	7.6±0.6b	7.1±0.6b
RBCC (×10^6·mm^{-3})	0.94±0.06a	0.83±0.06b	0.83±0.07b	0.61±0.07a*	0.55±0.07b*	0.52±0.07b*
MCHC (g·mL^{-1})	0.400±0.010	0.398±0.011	0.402±0.010	0.398±0.003	0.399±0.009	0.394±0.012
MCH (pg)	97.7±4.5	97.5±4.8	102.9±10.3	138.5±13.6*	145.7±15.1*	150.0±21.0*
MCV (fL)	24.9±1.0	24.4±0.9	24.9±1.8	35.5±3.4*	36.6±3.9*	37.0±4.4*

Note: Values are means ± standard error; $N = 11$ for diploids and $N = 9$ for triploids. Values that do not share a common letter within a given ploidy are significantly different from each other as determined by one-way repeated measures analysis of variance and pairwise Tukey's multiple comparison test ($p < 0.05$).

*Significantly different from "diploid" at given swimming speed as determined by Student's t test ($p < 0.05$).

fuged at 13 400*g* for 5 min, and used to determine hematocrit (Hct) and arterial CO_2 content (C_aCO_2) from the plasma fraction. The remaining blood was spun down as above and plasma removed for measurement of arterial plasma pH (pH_a) and later measurement of plasma lactate concentration. The plasma aliquot for determination of lactate was deproteinized with ice-cold 0.6 N perchloric acid, spun down as above, and the supernatant was frozen in liquid nitrogen and stored at –80 °C for later analysis.

Analytical techniques and calculations

The PO_2 of the water in the swim tube respirometer was continuously measured with a thermostatted PO_2 electrode (model E5046; Radiometer, Copenhagen, Denmark) and displayed on a PHM71 acid–base analyzer (Radiometer). The electrode was calibrated daily with air-saturated water. The analog output from the PHM71 meter was sampled at 1 Hz using the data acquisition system Labtech Notebook (Measurement Computing Corporation, Middleboro, Massachusetts, USA). MO_2 was calculated from the change in water PO_2 over the duration that the respirometer was sealed, taking into account the solubility of O_2 in seawater at 9 °C (Boutilier et al. 1984), the volume of the swim tunnel, and the volume occupied by the fish. For a given fish, the ratio of maximum to acclimation MO_2 within a swimming trial was used to determine the fold increase in MO_2. Measurements of P_aO_2 and C_aO_2 were made using thermostatted Radiometer PO_2 electrodes with PHM71 acid–base analysers. C_aO_2 was measured using the method described by Tucker (1967). C_aCO_2 was measured with a gas chromatograph (model III; Carle Instruments, Anaheim, California, USA) following the methods of Boutilier et al. (1985). The arterial partial pressure of CO_2 (P_aCO_2) and the plasma bicarbonate (HCO_3^-) concentration were calculated from C_aCO_2 and pH_a by rearrangement of the Henderson–Hasselbalch equation, with values of plasma pK and CO_2 solubility coefficients from Boutilier et al. (1984). pH_a and pH_i were measured using a thermostatted Radiometer G297/G2 glass capillary electrode with a PHM71 acid–base analyser. pH_i was measured according to the freeze–thaw method of Zeidler and Kim (1977). Whole-blood lactate concentration was measured spectrophotometrically using an NAD^+-linked enzymatic procedure (826-UV, Sigma). RBCC were performed on a Coulter Counter® model TAII (Coulter Electronics Ltd., Luton, England), and the accuracy of the counts was verified on six random samples using an improved Neubauer hemocytometer (Hesser 1960). Blood [Hb] was determined spectrophotometrically using a total Hb assay kit (525-A, Sigma). The mean cellular [Hb] (MCHC) was calculated from [Hb]/Hct, the mean cellular Hb content (MCH) from ([Hb]/RBCC)×10, and the mean RBC volume (MCV) from Hct/RBCC. Methemoglobin was determined using the method of Barlett et al. (1987). The percent saturation of Hb with O_2 (SO_2) was calculated as

$$\frac{C_aO_2 - (P_aO_2 \times \alpha O_2)}{[\text{Hb}] \times 4} \times 100$$

where C_aO_2 and Hb are in µmol·L^{-1} and αO_2, the solubility of O_2 at 9 °C and 29 ppt, is in µmol·L^{-1}·mmHg^{-1} (1 mmHg (0 °C) = 133.322 Pa) (Boutilier et al. 1984).

Statistics

All data are presented as means ± standard error. Differences between swimming speeds within a given ploidy were assessed by one-way repeated measures analysis of variance (ANOVA) followed by pairwise Tukey's multiple comparison test. Differences between ploidies at a given swimming speed were determined by Student's t test. The significance level for all statistical tests was $p < 0.05$.

Results

Throughout the exercise protocol, there was no difference between ploidies in Hct, Hb, and MCHC (Table 1). In contrast, the RBCC of triploids were significantly lower, and the MCH and MCV were significantly higher than those of diploids. In the diploid and triploid fish, the Hct, Hb, and RBCC at both 2 BL·s^{-1} and Ucrit were significantly lower than the control values obtained at the acclimation swimming speed of 0.4 BL·s^{-1}. Blood samples analyzed on the Neubauer hemocytometer and the Coulter Counter® gave equivalent RBCCs, the two methods differing by a maximum of 6%.

In diploid and triploid fish, MO_2 increased linearly with swimming speed, and with the exception of the 1.5 BL·s^{-1} values, MO_2 did not differ between ploidies throughout the exercise protocol (Fig. 1). Similarly, diploids and triploids

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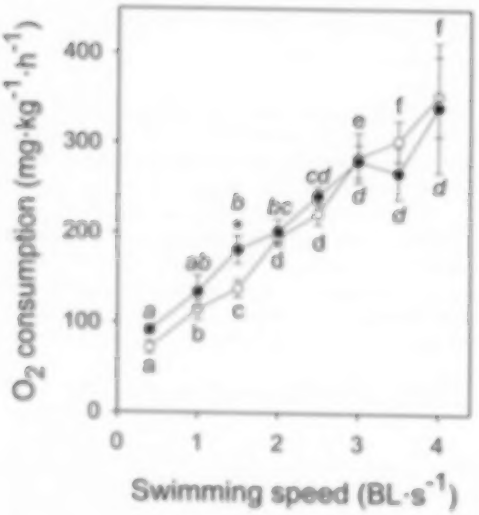
Fig. 1. Oxygen consumption as a function of swimming speed in diploid (open circle) and triploid (solid circle) chinook salmon (*Oncorhynchus tshawytscha*). Swimming speed is in body lengths ($BL \cdot s^{-1}$). Values that do not share a common letter within a given ploidy (italicized letters are used for the triploid group) are significantly different from each other as determined by one-way repeated measures analysis of variance and pairwise Tukey's multiple comparison test ($p < 0.05$). The asterisk (*) denotes a significant difference between ploidies at a given swimming speed as determined by Student's *t* test ($p < 0.05$). Values are means ± standard error; *N* values decrease with increasing swimming speed and range from 6–11 for diploids and 5–9 for triploids.



did not differ significantly in Ucrit or MO_2 max (Table 2). However, whereas 100% of the diploids maintained a swimming velocity of 3.5 $BL \cdot s^{-1}$ for 30 min, only 56% of the triploids did not fatigue at this swimming speed. Moreover, over the course of the swim performance test, the average increase in MO_2 was significantly higher in diploids than in triploids (Table 2). Also, while swimming speed did not affect C_aO_2 within a given ploidy, O_2 carrying capacity was significantly lower in triploids than in diploids at all sampling times (Fig. 2). At Ucrit, triploids also had significantly lower Hb–O_2 saturation and RBC pH than diploids, but similar P_aO_2 and methemoblobin values (Table 2).

With regards to CO_2 transport and acid–base balance, diploids and triploids did not differ in CO_2 content, P_aCO_2, plasma pH, or plasma lactate at the acclimation swimming speed, during sustained exercise, or at Ucrit (Figs. 3, 4). In both ploidies, an increase in swimming velocity had no significant effect on CO_2 content (Fig. 3*a*) but resulted in significant changes in P_aCO_2 (Fig. 3*b*), plasma pH (Fig. 4*a*), and plasma lactate (Fig. 4*b*). Relative to the values obtained at 0.4 $BL \cdot s^{-1}$ and 2.0 $BL \cdot s^{-1}$, exercise at the critical swimming velocity increased both P_aCO_2 and plasma lactate, but decreased plasma pH. The overall changes in acid–base balance observed during the exercise regime are shown in the pH / HCO_3^- plots of Fig. 5. In both ploidies, while changes in acid–base balance between the acclimation swimming speed and 2.0 $BL \cdot s^{-1}$ followed the blood buffer line, Ucrit was associated with a marked acidosis without an increase in plasma HCO_3^-.

Table 2. Maximal critical swimming velocity (Ucrit), O_2 consumption rate (MO_2) at the acclimation (acc) swimming speed, maximum MO_2, fold increase in MO_2 throughout the swim performance test, arterial O_2 partial pressure (P_aO_2), percent saturation of hemoglobin with O_2 (SO_2), percent methemoglobin (MetHb), and red blood cell intracellular pH (RBC pH_i) in diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*).

Parameter	Diploid	Triploid
Ucrit ($BL \cdot s^{-1}$)	3.92±0.12	3.60±0.22
MO_2 acc ($mg \cdot kg^{-1} \cdot h^{-1}$)	72.3±6.7	87.7±7.0
MO_2 max ($mg \cdot kg^{-1} \cdot h^{-1}$)	364.9±26.7	311.1±35.1
MO_2 fold increase	5.21±0.29	3.60±0.35*
P_aO_2 at Ucrit (mmHg)	95.3±5.9	94.3±6.9
SO_2 at Ucrit (%)	81.5±4.6	62.2±4.4*
MetHb at Ucrit (%)	3.2±0.9	1.8±0.5
RBC pH_i at Ucrit	7.49±0.01	7.42±0.02*

Note: Values are means ± standard error; $N = 11$ for diploids and $N = 9$ for triploids. BL, body length; 1 mmHg (0 °C) = 133.322 Pa.
*Significantly different from diploid for given parameter as determined by Student's *t* test ($p < 0.05$).

Discussion

While confirming that triploid and diploid salmonids have similar Ucrit and O_2 consumption rates, results from this study also clearly show that triploid chinook salmon have a reduced aerobic capacity relative to diploid fish from the same stock. In contrast, we found no evidence that triploidy affects CO_2 excretion or blood acid–base status either during aerobic swimming or at Ucrit.

Triploid chinook salmon, in agreement with previous hematological assessments of other salmonid species (e.g., Benfey 1999; Benfey and Biron 2000; Sadler et al. 2000), are characterized by having fewer but larger erythrocytes, a higher erythrocyte Hb content, and a similar Hct to diploids. Although some studies have observed that triploids have lower total blood [Hb] and (or) mean cellular [Hb] than diploids (Benfey and Sutterlin 1984*a*; Small and Randall 1989; Sadler et al. 2000), overall the effects of triploidy on these hematological parameters are equivocal (see Benfey 1999), and we observed no difference in either value between ploidies in this study. Similarly, while the blood sampling protocol significantly reduced Hct and total blood [Hb] over the course of the swimming trial, the magnitude of these changes did not differ between ploidies and were relatively small. Therefore, based solely on total blood [Hb], we expected diploid and triploid fish in this study to have equivalent maximal O_2 carrying capacities and aerobic scope.

As previously observed in coho salmon (*Oncorhynchus kisutch*; Small and Randall 1989) and brook trout (Stillwell and Benfey 1997), we found no difference between the swimming performance of triploid and diploid chinook salmon. Similarly, in accordance with several studies investigating the aerobic capacity of triploid salmonids (Benfey and Sutterlin 1984*b*; Oliva-Teles and Kaushik 1990; Yamamoto and Iida 1994), we observed similar MO_2 values

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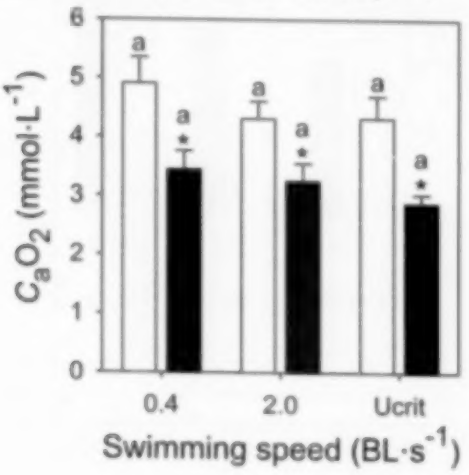
Fig. 2. Arterial O_2 content (C_aO_2) of diploid (open bar) and triploid (solid bar) chinook salmon (*Oncorhynchus tshawytscha*) swimming either at 0.4 body lengths (BL)·s^{-1} or 2.0 BL·s^{-1} or at maximal critical swimming velocity (Ucrit). Values that do not share a common letter within a given ploidy are significantly different from each other as determined by one-way repeated measures analysis of variance and pairwise Tukey's multiple comparison test ($p < 0.05$). An asterisk (*) denotes a significant difference between ploidies at given swimming speed as determined by Student's *t* test ($p < 0.05$). Values are means ± standard error; $N = 11$ for diploids and $N = 9$ for triploids.



for triploid and diploid chinook salmon during aerobic swimming and at Ucrit. In contrast, throughout the swimming trial, whereas the increase in metabolic rate and the C_aO_2 and SO_2 values in diploids were consistent with the data reported for other salmonids (Kiceniuk and Jones 1977; Brett and Groves 1979; Brauner et al. 2000*b*), triploids were characterized by significantly lower values. Overall, diploids had a 45% greater increase in MO_2 than did triploids over the course of the swim performance test, SO_2 at Ucrit was 24% less in triploids than in diploids, and on average the C_aO_2 of triploids was approximately 30% lower than that of diploids at all sampling times. Thus, despite having similar Ucrit and MO_2, our results clearly suggest that the aerobic capacity of triploid chinook salmon is more limited than their diploid counterpart.

Although the Ucrit test is traditionally used as an indicator of aerobic capacity in fish (Brett 1964; Hammer 1995), our results suggest that the critical swimming velocity test is not particularly sensitive to the arterial O_2 carrying capacity of the blood. This is consistent with the results of Brauner et al. (1993), who observed that Ucrit in chinook salmon is virtually independent of functional [Hb] until the latter is reduced to less than 51% of control level. Similarly, in rainbow trout that have an Hct within the normal range, increasing C_aO_2 has a very limited impact on Ucrit (Gallaugher et al. 1992, 1995). Overall, the relationship between Ucrit and C_aO_2 in fish may be weak because it can be influenced by several compensatory physiological adjustments (Brauner et al. 1993). For example, during exercise fish may compensate for a reduction in O_2 carrying capacity by increasing arterial–venous O_2 content, cardiac output, and ventilation volume and frequency (Kiceniuk and Jones 1977) by redistributing blood from the gut towards the aerobic red muscles (Thorarensen et al. 1993) or by recruiting the anaerobic white muscle fibers (Jones 1982). Whether the Ucrit value and the MO_2 of triploids in this study mask the recruitment of these or other compensatory mechanisms is not clear. While Altimiras et al. (2002) found no abnormalities in the cardiac performance of triploid brown trout swimming at Ucrit, a detailed study comparing the cardiovascular performance of swimming triploid and diploid salmonids from the same stock has yet to be performed. Similarly, while resting ventilation frequency may (King and Lee 1993) or may not (Stillwell and Benfey 1996) be higher in triploid than diploid salmonids, a comparison between ploidies during exercise of ventilation frequency and more importantly, ventilatory stroke volume (Jones and Randall 1978), has not been performed. In contrast, there is no evidence that triploids utilize anaerobic pathways to a greater extent than diploids following exhaustive exercise (Hyndman et al. 2003*a*, 2003*b*), and the plasma lactate values in this study suggest equal recruitment of anaerobic metabolism at Ucrit between ploidies. However, the extent to which triploids utilize anaerobic energy stores and clear lactate from tissues during sustained swimming and Ucrit remain to be characterized.

Our observation of in vivo triploid chinook salmon having a reduced C_aO_2 relative to diploids concurs with the in vitro results of Graham et al. (1985), who found a reduced Hb–O_2 loading ratio in Atlantic salmon blood. Although only measured at Ucrit, the lower erythrocytic pH of triploids will reduce the affinity of blood for O_2 (Bohr effect) and its maximal O_2 carrying capacity (Root effect). While the difference in erythrocytic pH between triploid and diploid chinook salmon at Ucrit is modest, in salmonids small changes in pH_i can have large effects on the O_2 carrying capacity of the blood (Pelster and Weber 1990; Brauner and Randall 1996). In Atlantic salmon at least, there appears to be no differences in Hb–O_2 affinity or in the magnitude of the Bohr and Root effects between diploid and triploid blood (Graham et al. 1985; Sadler et al. 2000). Similarly, we found no evidence that MetHb contributes to the reduced O_2 carrying capacity of triploids. At Ucrit, both ploidies had MetHb levels that were on par with previously reported values for resting chinook salmon (Brauner et al. 1993). Also, while RBC organic phosphates are powerful modulators of Hb–O_2 affinity in fish (Nikinmaa 1990), analysis of diploid and triploid Atlantic salmon erythrocytes has revealed no difference in organic phosphate concentrations (Graham et al. 1985; Sadler et al. 2000). Therefore, whereas many factors determine the amount of O_2 carried by a given amount of Hb in fish, few appear to contribute to the reduced O_2 carrying capacity of triploids. While the precise mechanism remains to be determined, our data suggest that differences in erythrocyte pH may be a contributing factor. Interestingly, triploid Atlantic salmon (King and Lee 1993) and brook trout (Benfey 1999) have a higher incidence of erythrocyte abnormalities than diploids, including cells with bisected nuclei and pinched cells. Whether chinook salmon blood also contains a higher proportion of deformed erythrocytes and whether these abnormal RBCs can transport O_2 is not known.

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Fig. 3. (*a*) Arterial CO_2 content (C_aCO_2) and (*b*) partial pressure (P_aCO_2) of diploid (open bar) and triploid (solid bar) chinook salmon (*Oncorhynchus tshawytscha*) swimming at either 0.4 body lengths (BL)·s^{-1} or 2.0 BL·s^{-1} or at maximal critical swimming velocity (Ucrit). Values that do not share a common letter within a given ploidy are significantly different from each other as determined by one-way repeated measures analysis of variance and pairwise Tukey's multiple comparison test ($p < 0.05$). Values are means ± standard error; $N = 11$ for diploids and $N = 9$ for triploids.

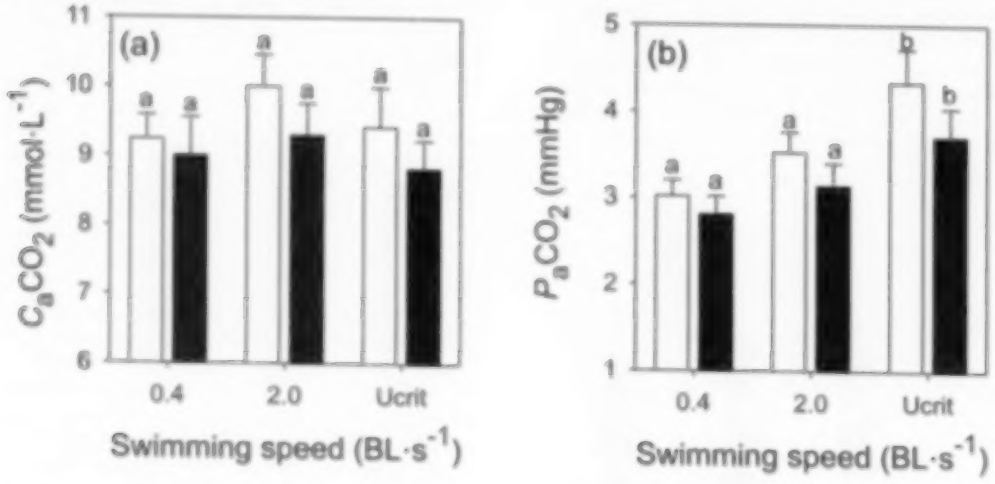
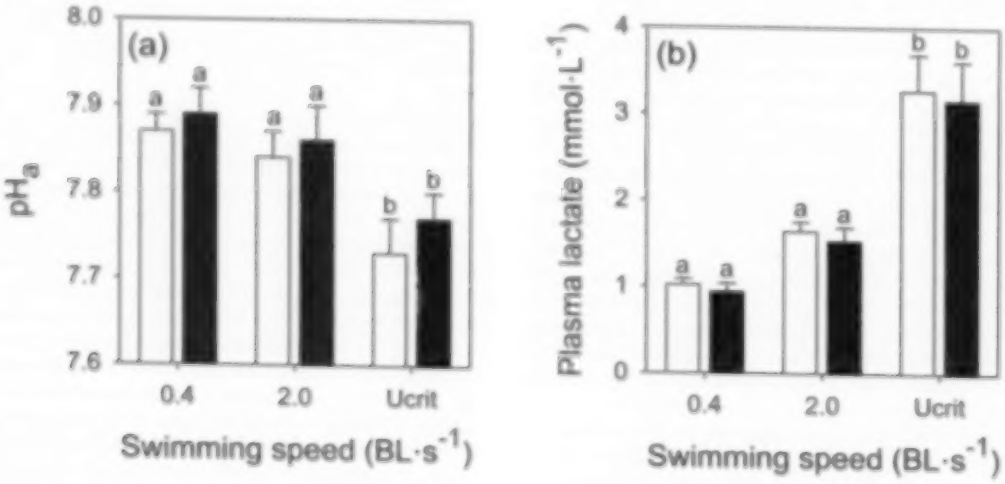


Fig. 4. (*a*) Arterial pH (pH_a) and (*b*) plasma lactate of diploid (open bar) and triploid (solid bar) chinook salmon (*Oncorhynchus tshawytscha*) swimming at either 0.4 body lengths (BL)·s^{-1} or 2.0 BL·s^{-1} or at maximal critical swimming velocity (Ucrit). Values that do not share a common letter within a given ploidy are significantly different from each other as determined by one-way repeated measures analysis of variance and pairwise Tukey's multiple comparison test ($p < 0.05$). Values are means ± standard error; $N = 11$ for diploids and $N = 9$ for triploids.



Available evidence also suggests that diffusion limitations to branchial O_2 transfer may contribute to the reduced aerobic capacity of triploid salmonids. For brook trout swimming at low speed, triploids take up less O_2 than diploids per opercular cycle (Stillwell and Benfey 1996). Moreover, although their findings have yet to be corroborated in other salmonid species, Sadler et al. (2001) showed that triploid Atlantic salmon have a significantly smaller gill surface area than diploids. The large increase in O_2 uptake during exercise in salmonids is achieved in part via a significant increase in the percentage of gill lamellae that are perfused (Randall and Daxboeck 1984). With a reduced gill surface area, the respiratory apparatus in triploids may have a smaller capacity than in diploids and, as shown in this study, a limited ability to increase gas exchange during exercise or other conditions that require an increase in O_2 uptake.

While several studies have compared the aerobic capacity of triploid and diploid salmonids (see above for discussion), to our knowledge this is the first study to report on CO_2 excretion in triploids. CO_2 excretion in fish depends primarily upon the dehydration of HCO_3^- by carbonic anhydrase within RBCs prior to gill blood entry (Brauner and Randall

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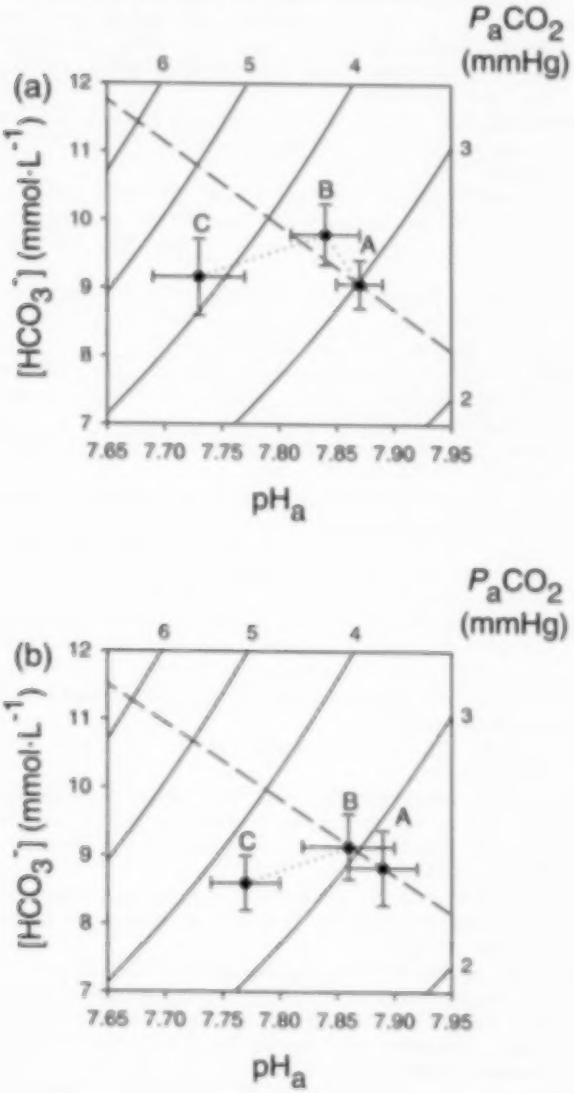
Fig. 5. A pH_a/HCO_3^- plot of changes in blood acid–base status of diploid (*a*) and triploid (*b*) chinook salmon (*Oncorhynchus tshawytscha*) swimming at either 0.4 body lengths ($BL \cdot s^{-1}$) (A) or 2.0 $BL \cdot s^{-1}$ (B) or at maximal critical swimming velocity (Ucrit; C). The isobars are for the arterial partial pressure of CO_2 (P_aCO_2) at 9 °C. The buffer lines (dotted lines) were calculated from the regression equation for β as a function of hemoglobin concentration ([Hb]) derived by Wood et al. (1982) and a [Hb] of 9.1 $g \cdot dL^{-1}$ for diploids and 8.1 $g \cdot dL^{-1}$ for triploids (the mean values measured at 0.4 $BL \cdot s^{-1}$). Values are means ± standard error; $N = 11$ for diploids and $N = 9$ for triploids.



1996) and at rest the rate-limiting step for CO_2 excretion is the rate of $HCO_3^- - Cl^-$ exchange at the surface of red cells (Perry et al. 1982). During exercise, CO_2 excretion may also be restricted by gill diffusion limitations (Thomas et al. 1987; Brauner et al. 2000*a*) and, as venous Hb–O_2 content falls, by the availability of erythrocytic Bohr protons (Brauner et al. 2000*b*). Therefore, in triploids, any effect of increased cell size on erythrocytic $HCO_3^- - Cl^-$ exchange or on the availability of protons for HCO_3^- dehydration could impair CO_2 excretion. Similarly, as discussed above, a reduction in gill surface area in triploids (Sadler et al. 2001) could limit CO_2 excretion during exercise. However, we observed no difference in C_aCO_2, P_aCO_2, or in arterial plasma HCO_3^- levels between triploid and diploid chinook salmon at any swimming speed. Moreover, throughout the exercise protocol, diploids and triploids were characterized by similar changes in C_aCO_2, P_aCO_2, and plasma HCO_3^-. In both ploidies, there was no significant change in CO_2 transport between the acclimation swimming speed and 2.0 $BL \cdot s^{-1}$, and as previously observed in diploid rainbow trout (Thomas et al. 1987), a significant increase in P_aCO_2 at Ucrit. Therefore, despite their larger size, reduced Hb–O_2 content, and slightly lower pH, triploid RBCs appear to play a similar role in CO_2 excretion as their diploid counterpart.

Triploid and diploid chinook salmon also experienced similar acid–base disturbances throughout the swim performance test. As previously observed in rainbow trout during aerobic swimming (Thomas et al. 1987; Brauner et al. 2000*a*), relative to the acid–base status of the fish swimming at the acclimation speed, the pH_a/HCO_3^- plots show that both diploid and triploid fish swimming at 2.0 $BL \cdot s^{-1}$ experienced a small respiratory acidosis. At Ucrit, in contrast, both ploidies experienced a marked respiratory and metabolic acidosis. The significant increase in P_aCO_2 at Ucrit was accompanied by the recruitment of anaerobic metabolism as indicated by the arterial acidosis and the significant increase in plasma lactate. These results are consistent with the observations of Jones (1982) and Burgetz et al. (1998), who estimated that salmonids gradually recruit anaerobic white muscle fibers once their swimming speed surpasses 70%–80% of Ucrit.

In summary, CO_2 transport and acid–base balance in chinook salmon either during aerobic swimming or at Ucrit do not appear to differ from that of their diploid counterpart. Moreover, as previously observed in other salmonid species (Small and Randall 1989; Stillwell and Benfey 1996; Benfey 1999), based solely on Ucrit and O_2 consumption rates, it appears that aerobic capacity may not differ between triploids and diploids. However, a more in-depth examination of O_2 transport parameters clearly shows that triploid chinook salmon have a lower O_2 carrying capacity than diploids. Larger cells mean longer diffusion distances, but this does not appear to be limiting exercise, as triploid and diploid fish can achieve the same swimming speeds. For similar reasons, blood O_2 content also does not seem to be limiting swimming speed in these animals. Thus O_2 transport may not be limiting swimming speed in these fish. What then does limit swimming speed? Perhaps some intrinsic property of the muscle, rather than O_2 delivery, determines swimming speed in these fish under favorable environmental conditions. Therefore, while the specific mechanisms are mostly unknown (however see Mercier et al. 2002), our results suggest that triploids are able to compensate for their reduced aerobic capacity under the current exercise regime. Although such compensatory measures may mask limitations in the aerobic capacity of triploids under favourable thermal regimes, the effects of triploidy on O_2 transport might contrib-

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ute to the inferior physiological performance of triploid salmonids reared under suboptimal conditions.

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Anik Giguère, Peter G.C. Campbell, Landis Hare, D. Gordon McDonald, and Joseph B. Rasmussen	**1702–1716**	Influence of lake chemistry and fish age on cadmium, copper, and zinc concentrations in various organs of indigenous yellow perch (*Perca flavescens*)
M.A. Gray, R.A. Cunjak, and K.R. Munkittrick	**1717–1722**	Site fidelity of slimy sculpin (*Cottus cognatus*): insights from stable carbon and nitrogen analysis
J.A. Miller and A.L. Shanks	**1723–1735**	Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design
Nicholas E. Jones and William M. Tonn	**1736–1746**	Resource selection functions for age-0 Arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation
Dag Ø. Hjermann, Nils Chr. Stenseth, and Geir Ottersen	**1747–1755**	The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data
Gregory T. Ruggerone and Frederick A. Goetz	**1756–1770**	Survival of Puget Sound chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*)
A. Jamie F. Gibson and Ransom A. Myers	**1771–1783**	Estimating reference fishing mortality rates from noisy spawner–recruit data
Christopher J. Egertson and John A. Downing	**1784–1796**	Relationship of fish catch and composition to water quality in a suite of agriculturally eutrophic lakes
Nicholas J. Bernier, Colin J. Brauner, John W. Heath, and David J. Randall	**1797–1805**	Oxygen and carbon dioxide transport during sustained exercise in diploid and triploid chinook salmon (*Oncorhynchus tshawytscha*)

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

G.A. Rose **1553–1557** Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years

ARTICLES / ARTICLES

K. Brander and R. Mohn **1558–1564** Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*)

Elisabeth I. Meyer and Rainer Poepperl **1565–1581** Assessing food-web structure, matter fluxes, and system attributes of a Central European mountain stream by performing mass-balanced network analysis

Jonathan W. Moore and Daniel E. Schindler **1582–1589** Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*)

Alex Haro, Theodore Castro-Santos, John Noreika, and Mufeed Odeh **1590–1601** Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers

Theodore Castro-Santos **1602–1615** Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers

Michael A. Etnier **1616–1626** Reevaluating evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens

Calum MacNeil, John Prenter, Mark Briffa, Nina J. Fielding, Jaimie T.A. Dick, Gillian E. Riddell, Melanie J. Hatcher, and Alison M. Dunn **1627–1635** The replacement of a native freshwater amphipod by an invader: roles for environmental degradation and intraguild predation

David C. Hardie and Paul D.N. Hebert **1636–1646** Genome-size evolution in fishes

T.R. Hammond **1647–1657** A recipe for Bayesian network driven stock assessment

Eric A. Parkinson, John R. Post, and Sean P. Cox **1658–1670** Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery

Johanne Dalsgaard and Michael St. John **1671–1680** Fatty acid biomarkers: validation of food web and trophic markers using ^{13}C-labelled fatty acids in juvenile sandeel (*Ammodytes tobianus*)

Continued on inside back cover / Suite au verso

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